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Estimation of Annual and Semi-Annual Survival of Adult Female Blue Crabs and Assessment of the Effectiveness of the Virginia Blue Crab Sanctuary using Tag-Return Methodology

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ESTIMATION OF ANNUAL AND SEMI-ANNUAL SURVIVAL OF ADULT
FEMALE BLUE CRABS AND ASSESSMENT OF THE EFFECTIVENESS OF THE
VIRGINIA BLUE CRAB SANCTUARY USING TAG-RETURN METHODOLOGY

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Science


by

Debra M. Lambert

2005

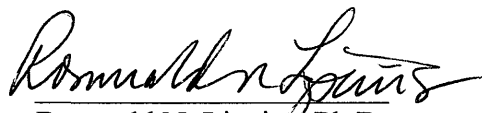
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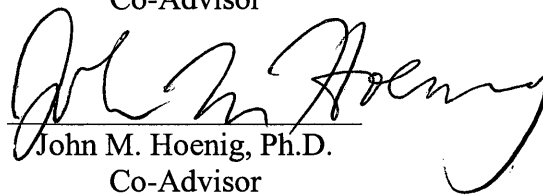


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PREFACE

Chapter 2 of this thesis will be submitted to Fisheries Bulletin and is thus formatted under the guidelines specified by that journal. Chapter 3 of this thesis was submitted to Marine Ecology Progress Series for consideration of publication on October 8, 2005 and is thus formatted under the guidelines specified by that journal.

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ABSTRACT

The blue crab fishery is the most valuable commercial fishery in Chesapeake Bay. The Chesapeake Bay stock recently experienced a period of overfishing, which has resulted in below average abundances, and the spawning stock has experienced an 84 % decline in biomass relative to levels in the late 1980s. The status of the stock is determined by comparing current estimates of mortality to biological reference points. Given the current focus on blue crab conservation, there is a need to obtain reliable, empirical estimates of survival to compare to the biological reference points. A tagging program was initiated on the terminally-molted, mature female component of the Bay-wide blue crab stock to estimate annual and semi-annual survival rates and to assess the effectiveness of the Virginia blue crab spawning sanctuary. Crabs were obtained from five fishery-independent research surveys throughout Chesapeake Bay and were measured, tagged, and released on-site. Tagging was conducted primarily during winter (late October to March) and summer (May to August) from November 2001 to March 2005. Recaptures of tagged crabs were reported by commercial and recreational fishers.

Annual survival rates and tag recovery rates were estimated independently for the winter and summer tagging data using a Brownie model. The two independent estimates of annual survival based on winter tagging (0.08 ± 0.02 SE) and summer tagging (0.08 ± 0.02 SE) data were virtually identical and very low. The estimated tag recovery rate was 24 % based on the winter tagging data and 17 % based on the summer tagging data. The estimated monthly survival rate during winter, 0.87 ± 0.02 SE, was significantly higher than the monthly survival rate during summer, 0.74 ± 0.02 SE. The low estimates of annual survival are consistent with (i) historical estimates of the percentage of age 2+ females in the winter dredge fishery, and (ii) recent estimates of survival derived from estimates of exploitation rate obtained from the ratio of catch to pre-season abundance.

To assess the effectiveness of the spawning sanctuary, mature females were tagged and released inside and outside the sanctuary in the summers of 2002, 2003 and 2004. A comparison of the probability of recapture for crabs tagged outside the sanctuary to crabs tagged inside the sanctuary using relative risk provided a means of assessing the sanctuary effectiveness quantitatively. Probability of recapture for crabs released outside of the sanctuary was 6.3, 5.2, and 2.8 times the probability of recapture for crabs tagged inside the sanctuary for 2002, 2003 and 2004, respectively. Consequently, a significant proportion of adult female blue crabs remained in the sanctuary to spawn and was not captured by the fishery. Hence, the blue crab spawning sanctuary in Chesapeake Bay is an effective means of protecting females migrating to or residing in the spawning grounds.

These findings indicate that survival rates of mature female blue crabs in Chesapeake Bay have remained extremely low during a period of low abundance, which may be preventing stock recovery. Although the blue crab sanctuary is effective in

protecting the females that have entered its borders, it only offers protection for 3.5 months of the year. A low annual survival rate suggests that very few adult females live long enough to spawn in more than one year. Current management must be altered for sustainable exploitation of the blue crab in Chesapeake Bay. This study represents one of the few to derive field estimates of semi-annual survival of an invertebrate species using Brownie models. This investigation also serves as one of the few empirical tests to date of the effectiveness of a marine reserve designed to protect spawning stock.

CHAPTER 1: INTRODUCTION AND MOTIVATION

CHAPTER 1: INTRODUCTION AND MOTIVATION

The blue crab, *Callinectes sapidus* Rathbun, inhabits coastal and estuarine areas along the Atlantic coast of North and South America from Cape Cod to northern Argentina (Williams 1984). Mating occurs only once in the life of a female crab, after the female undergoes a terminal molt (Van Engel 1958, Millikin & Williams 1984). The mating season in Chesapeake Bay is from early May to October with peaks in May and late August or early September (Van Engel 1958). After maturing and mating, female crabs migrate down the Bay in the fall and over-winter in the southern portion of the Bay (Churchill 1919, Van Engel 1958). If mating occurs in early May, the first egg mass could be laid in August. For those females that mate in August and September, egg-laying is delayed until the following spring (Van Engel 1958).

The blue crab is an important species to the ecology and economy of Chesapeake Bay. Commercial harvesting of the blue crab occurs year around. A winter dredge fishery occurs in the mainstem of the Virginia portion of the Bay from 1 December to 31 March. A crab pot fishery occurs during the remainder of the year in the mainstem and tributaries of the Virginia portion of the Bay. The crab season in Maryland is from 1 April to 15 December. Crab pots are used in the mainstem of the Maryland portion of the Bay while trotlines are used in the tributaries. Crab scrapes are used in seagrass beds in Virginia and Maryland to capture peeler (crabs showing signs of imminent molting) and soft crabs in spring and summer. In addition, peeler pots (crab pots baited with an adult

male crab) are used to capture mate-seeking female peeler crabs. Peeler crabs are then held in shedding tanks until molting occurs and are then sold as soft crabs. There is little information available on the recreational harvest of blue crabs in the Bay.

The total dockside value of the commercial harvest in the Bay was approximately US \$53 million in 2003 (Personal communication, National Marine Fisheries Service, Fisheries Statistics Division, Silver Spring, MD). The three-year average (2002-2004) commercial harvest in the Bay of 54 million lbs is 26 % below the long-term (1968-2004) average harvest of 73 million lbs (Chesapeake Bay Stock Assessment Committee 2005). The Chesapeake Bay stock experienced a period of overfishing from 1998-2002 (Miller et al. 2005) which has resulted in below average abundances, and the spawning stock has experienced an 84 % decline in biomass relative to levels in the late 1980s (Lipcius & Stockhausen 2002).

In 2001, the Bi-state Blue Crab Advisory Committee (BBCAC) of the Chesapeake Bay Commission recommended that fisheries management agencies (Potomac River Fisheries Commission, Maryland Department of Natural Resources, and Virginia Marine Resources Commission) adopt a fishing mortality threshold and fishing mortality target that preserve a minimum of 10 % ($F_{10\%} = 1.0$) and 20 % ($F_{20\%} = 0.7$) of spawning potential, respectively (BBCAC 2001). To estimate these quantities it was necessary to assume a value for the instantaneous natural mortality rate, M . The status of the Chesapeake Bay blue crab stock has been determined by comparing current estimates of fishing mortality to these biological reference points.

Currently, estimates of fishing mortality rates are derived from estimates of exploitation rates. Exploitation rates (u) are based on comparing total catch during the

year to estimates of abundance at the start of the year of legal size animals and animals that will become legal size during the year. Abundances are determined from the Bay-wide dredge survey and u from the formula: $u = \text{catch}/\text{initial abundance}$ (Sharov et al. 2003). The estimates of exploitation rate are then converted into estimates of instantaneous fishing mortality rate (F) by assuming a value for the natural mortality rate (M) and a type II (continuous) fishery. That is, Sharov et al. (2003) solved the following equation iteratively for F :

$$u = \left(\frac{F}{F + M} \right) \times \left(1 - e^{-(F+M)} \right). \quad (1)$$

Sharov et al. (2003) used the value of 0.375 yr^{-1} for M , in line with a value of M used in the previous Chesapeake Bay blue crab stock assessment (Rugolo et al. 1998). Estimates of fishing mortality obtained from this method were compared to the target and threshold values (which were also determined assuming $M = 0.375 \text{ yr}^{-1}$) to determine if overfishing was occurring. Although the exploitation rate method appears the most appropriate to estimate F , it is heavily dependent on estimates of natural mortality rate, gear efficiency (used to estimate initial abundance), and total catch.

Given the focus on target and threshold fishing mortality rates there is a need to obtain reliable estimates of survival to compare to these biological reference points. This stems from the fact that the value of natural mortality used in the calculations (0.375 yr^{-1}) was obtained by consensus opinion rather than measured in the field. Tag-return studies using analytical models of the Brownie type can be used to obtain robust estimates of annual survival (Brownie et al. 1985). Tagging based estimates of survival can be compared to the mortality estimates obtained by the exploitation rate method.

However, the determination of overall survival rates can also provide insight into the natural mortality rate. This is because equation (1) can be rewritten as:

$$u = \frac{F}{-\ln S} (1 - S). \quad (2)$$

Hence, given estimates of u from the Bay-wide dredge survey and S from the tagging data, one can solve for fishing mortality, F . Then given F and S , one can solve for M as:

$$M = -\ln S - F. \quad (3)$$

It should be noted that the estimate of u is for the exploitable population of females while the estimate of S is for terminally molted (adult) females. The two estimates may not be strictly comparable but these are the only estimates available. Results concerning M will be presented in chapter 2. It should be noted that in the recent stock assessment for the blue crab in Chesapeake Bay (Miller et al. 2005), a new value of $M = 0.9 \text{ yr}^{-1}$ was adopted based in part on results from the blue crab tagging study described in chapter 2.

Tagging information can also provide direct estimates of the effectiveness of marine reserves, such as that designed to protect the blue crab spawning stock in Chesapeake Bay. A spawning sanctuary of 37,814 ha was established in the southern portion of the Bay in 1941 (Rob O'Reilly, Virginia Marine Resources Commission (VMRC), personal communication). In 1994, the Bayside Eastern Shore Sanctuary (BESS) was established to include an additional 19,400 ha along the eastern shore of the lower Bay, which was later reduced to 16,000 ha in 1998 (Seitz et al. 2001). In June of 2000, the sanctuary was expanded from the mouth of the Bay to the Virginia/Maryland border, roughly following the 10.7 m depth contour in the mainstem of the Bay, to a size of 172,235 ha (Lipcius et al. 2003). The purpose of the expansion was not only to protect

those female crabs in the spawning grounds but also to protect adult females en route to the spawning grounds during the reproductive period. The Virginia blue crab sanctuary was enlarged again in 2002, roughly following the 9.1 m depth contour, to its current size of 240,092 ha (VMRC Regulation # 4 VAC 20-752-10 ET SEQ). Commercial crab harvesting is prohibited in the sanctuary area between 1 June and 15 September; recreational crabbing is lawful only in the lower Bay area of the sanctuary.

The effectiveness of the current sanctuary has not been addressed. The second major portion of this thesis (Chapter 3) was therefore designed to quantify the effectiveness of the sanctuary in protecting mature females either en route to or within the sanctuary borders. The effectiveness of the sanctuary is in part determined by the degree and nature of crabs' mobility relative to the size and shape of the sanctuary. The effectiveness of the sanctuary is dependent on female crabs remaining in the sanctuary for spawning, and would be reduced if females were to move outside of the sanctuary prior to spawning and become captured by the fishery. A comparison of tag return rates from animals tagged inside and outside the spawning sanctuary thus provides a means to examine the effectiveness of the sanctuary.

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CHAPTER 2: TAG-RETURN ESTIMATION OF ANNUAL AND SEMI-ANNUAL
SURVIVAL RATES OF ADULT FEMALE BLUE CRABS

CHAPTER 2: TAG-RETURN ESTIMATION OF ANNUAL AND SEMI-ANNUAL SURVIVAL RATES OF ADULT FEMALE BLUE CRABS

ABSTRACT

The status of the Chesapeake Bay blue crab stock is determined by comparing current estimates of fishing mortality to biological reference points. Given the current focus on blue crab conservation, there is a need to obtain reliable estimates of survival to compare to the biological reference points. A tagging program was initiated on the terminally-molted, mature female component of the Bay-wide blue crab stock to estimate annual and semi-annual survival rates. Crabs were obtained from five fishery-independent research surveys throughout Chesapeake Bay and were measured, tagged, and released on-site. Tagging was conducted primarily during winter (late October to March) and summer (May to August) from November 2001 to March 2005. Annual survival rates and tag recovery rates were estimated independently for the winter and summer tagging data using a Brownie model. The two independent estimates of annual survival based on winter tagging (0.08 ± 0.02 SE) and summer tagging (0.08 ± 0.02 SE) data were virtually identical and very low. The estimated tag recovery rate was 24 % based on the winter tagging data and 17 % based on the summer tagging data. The estimated monthly survival rate during winter, 0.87 ± 0.02 SE, was significantly higher than the monthly survival rate during summer, 0.74 ± 0.02 SE. The low estimates of annual survival are consistent with (i) historical estimates of the percentage of age 2+ females in the winter

dredge fishery, and (ii) recent estimates of exploitation rate obtained from the ratio of catch to pre-season abundance. These findings indicate that survival rates of mature female blue crabs in Chesapeake Bay have remained extremely low during a period of low abundance, which may be preventing stock recovery. Moreover, this study represents one of the few to derive experimental Brownie model estimates of semi-annual survival of an invertebrate species subject to a continuous fishery.

INTRODUCTION

Blue Crab Fishery

The blue crab, *Callinectes sapidus* Rathbun, fishery is the most important commercial fishery in Chesapeake Bay and produces the highest landings of blue crabs in the United States (Miller et al.¹). The 2002-2004 average annual commercial landings in the Bay (24,500 MT) was 26 % below the long-term (1968-2004) average landing of 33,100 MT (Chesapeake Bay Stock Assessment Committee²). The Chesapeake Bay stock experienced a period of overfishing from 1998-2002 (Miller et al.¹), which has resulted in below average abundances, and the spawning stock has experienced an 84 % decline in biomass relative to levels in the late 1980s (Lipcius and Stockhausen, 2002).

In 2001, the Bi-state Blue Crab Advisory Committee (BBCAC) of the Chesapeake Bay Commission recommended that fisheries management agencies (Potomac River Fisheries Commission, Maryland Department of Natural Resources, and Virginia Marine Resources Commission) adopt a fishing mortality threshold and fishing mortality target that preserve a minimum of 10 % ($F_{10\%} = 1.0$) and 20 % ($F_{20\%} = 0.7$) of spawning potential, respectively, and a biomass threshold (equivalent to the lowest recorded stock abundance; BBCAC³). The status of the Chesapeake Bay blue crab stock

¹ Miller, T. J., S. J. D. Martell, D. B. Bunnell, G. Davis, L. Fegley, A. Sharov, C. Bonzek, D. Hewitt, J. Hoenig, and R. N. Lipcius. 2005. Stock Assessment of the blue crab in Chesapeake Bay 2005. Technical report series No. TS-487-05 of the University of Maryland Center for Environmental Science. National Oceanic and Atmospheric Administration (NOAA) Chesapeake Bay Office, 410 Severn Avenue, Suite 107, Annapolis, MD 21403.

² Chesapeake Bay Stock Assessment Committee 2005. 2005 Chesapeake Bay blue crab advisory report. Available from NOAA Chesapeake Bay Office, 410 Severn Avenue, Suite 107, Annapolis, MD 21403.

³ BBCAC. 2001. Taking action for the blue crab: managing and protecting the stock and its fisheries. Chesapeake Bay Commission. 60 West Street, Suite 200, Annapolis, MD 21401.

is determined by comparing current estimates of fishing mortality and abundance to these biological reference points. All regulatory authorities have taken actions since 2001 to reduce fishing mortality.

Blue crab mortality

Blue crab stock assessment has been hampered by incomplete catch and effort statistics and uncertainty over maximum age and natural mortality rate (Rugolo et al., 1998). The lack of a suitable method for aging crabs largely rules out the option of using age-based methods to estimate total mortality. Until recently, instantaneous mortality rates (Z) have been assessed from length-frequency distributions (Rugolo et al., 1998) using a model that is heavily dependent on assumptions of equilibrium conditions, known growth rates, and non-size-selective harvesting. Recently, there has been a switch in methodology to estimates of exploitation rate (u) based on comparing total catch during the year to estimates of abundance at the beginning of the year of legal size animals and animals that will become legal size during the year. Abundances are determined from the Bay-wide winter dredge survey; relative abundance (# of crabs caught per m^2) is converted to an estimate of absolute abundance by dividing by the gear efficiency and then extrapolating to the total survey area (Sharov et al., 2003). The total annual catch is based on commercial landings data that is converted from weight to number of crabs. The estimates of exploitation rate, $u = \text{catch}/\text{initial abundance}$, are then converted into estimates of instantaneous fishing mortality rate (F) by assuming a value for the natural mortality rate (M) and a type II (continuous) fishery. That is, Sharov et al. (2003) solved the following equation iteratively for F :

$$u = \left(\frac{F}{F + M} \right) \times (1 - e^{-(F+M)}).$$

Sharov et al. (2003) used the value of 0.375 yr^{-1} for M , in line with the value of M used in the previous Chesapeake Bay blue crab stock assessment (Rugolo et al. 1998). Estimates of fishing mortality obtained from this method are compared to the target and threshold values to determine if overfishing is occurring.

The new methodology is dependent on estimates of natural mortality rate, gear efficiency (used to estimate initial abundance), and total catch. The Chesapeake Bay Stock Assessment Committee (CBSAC) has endorsed the replacement of the length-based method with the exploitation rate method for the estimation of F . Although the exploitation rate method appears the most appropriate, the natural mortality rate remains poorly known and controversial. This stems from the fact that the value of natural mortality used in the calculations (0.375 yr^{-1}) was estimated by: $3/t_{\max}$, where t_{\max} is the maximum age of blue crabs, which was assumed to be 8 years (Rugolo et al. 1998). A maximum age of 8 years, however, is unlikely for the blue crab. In addition, recent work has shown that the $3/t_{\max}$ approach should be abandoned (Hewitt and Hoenig, 2005). The most recent stock assessment suggests that a value for M of 0.9 yr^{-1} is more reasonable than 0.375 yr^{-1} (Miller et al.¹).

Given the current focus on blue crab conservation (Seitz et al., 2001; Lipcius et al., 2001; Lipcius and Stockhausen, 2002; Lipcius et al., 2003) and the target and threshold fishing mortality rates (Miller et al.¹; CBSAC²; BBCAC³), there is a need to obtain reliable current estimates of survival to compare to these biological reference points. Tag-return studies using analytical models of the Brownie type can be used to obtain robust estimates of annual survival (Brownie et al., 1985). In addition, Brownie et

al. (1985) and Hearn et al. (1998) have shown that if tagging occurs more than once per year, it is possible to divide the total mortality estimates into their temporal components.

Mature female blue crabs are ideal for tag-return studies because they do not molt (Churchill, 1919; Van Engel, 1958) so tag loss can be assumed to be minimal. The shape of the carapace is such that a light-weight and non-invasive tag can easily be attached around the lateral spines on the dorsal surface. Tag-return studies on the blue crab have been used to examine migration (Fischler and Walburg, 1962; Turner et al., 2003; Aguilar et al., 2005; and references therein), to provide estimates of population size (Fischler, 1965), and to assess the effectiveness of protected areas (Medici, 2004; see chapter 3). The objective of this study was to estimate annual and semi-annual survival rates of adult female blue crabs in Chesapeake Bay through tag-return methods.

METHODS

Tagging protocol

Mature female crabs were captured, tagged and released by several fishery independent research surveys from November 2001 to March 2005. In winter (28 October to 13 March), crabs were tagged by the Bay-wide winter dredge survey, Virginia Institute of Marine Science (VIMS) Trawl Survey, and VIMS Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) survey. In summer (17 May to 28 August), crabs were tagged by the VIMS Trawl Survey, Maryland Department of Natural Resources (MDNR) Trawl Survey, and VIMS ChesMMAP Survey. The Chesapeake Biological Laboratory (CBL) Chesapeake Bay Fishery Independent

Multispecies Fisheries Survey (CHESFIMS) also tagged crabs in the summer of 2004. Winter tagging took place from 28 October 2001 to 13 March 2002, 28 October 2002 to 13 March 2003, 28 October 2003 to 13 March 2004, and 28 October 2004 to 13 March 2005. Summer tagging occurred from 17 May to 28 August of 2002, 2003, and 2004.

Crabs were measured (carapace width, spine tip to spine tip) with vernier calipers and tagged by tying a strap tag across the back and around the lateral spines; the ends were crimped together with a 0.635 cm, zinc-plated-copper, oval sleeve (mean weight of tag and crimp = 1.27 ± 0.06 g (\pm SD)). Crabs were then released as close as possible to the capture location. Each tag had an individual identification number, a toll-free phone number, the words "\$20 REWARD" and instructions to record the location and date of capture. An informational flyer was sent in February 2004 to all licensed crab fishers in Virginia to inform them of the tagging program. Newspaper articles in the Waterman's Gazette (published by the Maryland Watermen's Association) also publicized the program regularly since July 2004.

Captures of tagged crabs were reported by commercial and recreational fishers, who either left a message on the tag reporting phone line or spoke directly with staff at VIMS. I obtained as much of the following information over the phone as possible: location of capture, date of capture, water depth, method of capture, presence or absence of an egg mass, and whether the fisher was commercial or recreational. A letter describing the program with the corresponding crab release information, a data sheet, a map of Chesapeake Bay, and a self-addressed stamped envelope were mailed to the fisher with instructions to make any additional comments, to mark the location of the capture,

and to return the data forms and tag back to VIMS. Once the tag was received, payment was mailed to the fisher.

One caveat to the tagging procedure is that during the winter of 2002, the majority of the tags used (520 of 537) were labeled with “Reward” rather than “\$20 Reward.” We do not think this greatly affected the recovery rate since the tagging program was a year old at this point, fishers were already aware of the US \$20 reward, and the tag recovery rate did not differ significantly across years (see Results).

Survey Design

The Bay-wide winter dredge survey is conducted annually throughout Chesapeake Bay from November to March by VIMS and MDNR. The survey design follows a stratified random design that divides the Bay into three geographic strata: upper, middle, and lower Chesapeake Bay. A Virginia crab dredge (width 1.83 m) lined with a plastic mesh (1.3 cm) is towed along the bottom for 1 min at ~3 knots at approximately 1500 sites each season (Sharov et al., 2003).

The VIMS Trawl Survey samples monthly in the Virginia portion of the Bay and in the James, York, and Rappahannock Rivers. The survey deploys a 9.14 m semi-balloon otter trawl and tows for 5 min at approximately 100 sites monthly according to a combined fixed and stratified random sampling design (Montane et al.⁴). The MDNR Trawl Survey samples 37 fixed sites in six river systems (Chester River, Eastern Bay, Choptank River, Patuxent River, Tangier Sound, and Pocomoke Sound) and 12 trial sites

⁴ Montane, M. M., W. A. Lowery, and H. M. Austin. 2004. Estimating relative juvenile abundance of ecologically important finfish and invertebrates in the Virginia portion of Chesapeake Bay, 106 p. Project # NA03NMF4570378, June 2003 - May 2004. Annual Report to NOAA Chesapeake Bay Office. Virginia Institute of Marine Science, PO Box 1346, Gloucester Pt., VA 23062.

in three river systems (Fishing Bay, Little Choptank, and Nanticoke) monthly from May through November using a 4.9 m semi-balloon otter trawl.

The VIMS ChesMMAAP survey samples the entire mainstem of Chesapeake Bay, stratifying the bay into five regions with three depth strata per region. The survey deploys a 13.7 m otter trawl and tows at approximately 3.5 knots for 20 min per site. Five cruises are conducted each year (March, May, July, September, and November) and approximately 90 sites are sampled per cruise (Latour et al., 2003).

The CHESFIMS survey conducts three cruises a year (spring, summer, and fall) and samples approximately 50 sites per cruise throughout the mainstem of the Bay according to a combined fixed and stratified random sampling design. The survey uses a single, oblique stepped midwater trawl (18 m²) (Miller et al.⁵).

Survival estimation

A Brownie-type model (Brownie et al., 1985) was used to estimate annual survival. Briefly, the rationale of tagging studies is that if two cohorts of animals are tagged, one at the start of year 1 and one at the start of year 2, then during year 2 we would expect to get equal fractions of tags returned from the two cohorts except for the fact that the first cohort has been at liberty for an extra year and has thus experienced an extra year of mortality, which reduces the number of tag returns. The tag return data are described within two triangular shaped matrices in terms of the observed and expected

⁵ Miller, T. J., K. Curti, D. Loewensteiner, A. F. Sharov, J. A. Nye, B. Muffley, M. C. Christman, J. H. Volstad, and E. D. Houde. 2004. Abundance, distribution and diversity of Chesapeake Bay Fishes: Results from CHESFIMS (Chesapeake Bay Fishery Independent Multispecies Fisheries Survey). Chesapeake Bay Fisheries Research Program Symposium Report 2003. NOAA Chesapeake Bay Office, 410 Severn Avenue, Suite 107, Annapolis, MD 21403.

number of recaptures from each tagged cohort in each year (Table 1). The matrix of observed data is expressed as $R = [r_{ij}]$, where r_{ij} is the number of crabs recovered in year j from crabs tagged in year i . The second matrix contains the expected values for the recapture of tagged individuals. The probability of recapturing a tagged individual is based on two parameters, an annual survival rate (S) and the tag recovery rate (f), which is the rate at which tagged individuals are recovered and reported. The structure of the model used to estimate these parameters will depend on the assumptions relating to the parameters. For example, under the assumption that recovery and survival rates are year specific (referred to as model 1 by Brownie et al. (1985)), the expected recaptures will be modeled as shown in Table 1. The observed value r_{ij} is replaced with $E(r_{ij})$, where $E(\cdot)$ denotes expectation. In this model, the probability of recapturing a crab in year j that was tagged in year i is expressed as a function of the number of crabs tagged in year i (N_i), the tag recovery rate in year j (f_j), and the cumulative annual survival rate through year $j-1$ (defined to be 1.0 for $j = i$).

The recaptures from each tagged cohort are viewed as a random sample from an independent multinomial distribution. The likelihood function is therefore the product of the multinomials from all the cohorts. The values of the parameters that maximize the likelihood function are then calculated and are referred to as the maximum likelihood estimates (MLEs) of the parameters.

Once-a-year tagging models and model selection

Four Brownie models were fitted separately to both the winter and summer tag-return data. The winter tagging data contained four tagged cohorts and four years of

recapture, while the summer tagging data contained three tagged cohorts and three years of recapture. The four models and their assumptions are as follows: (1) model S_b, f_t where S and f vary with time, (2) model S, f_t where the survival rate is constant while the recovery rate varies over time, (3) model S_b, f where the survival rate varies over time and the recovery rate is constant, and (4) model S, f where both the survival and recovery rates are constant over time. Model S_b, f_t is the most general model and allows for the most parameters while model S, f is a simpler and more restrictive model.

Parameter estimates were obtained for each model described above, using maximum likelihood estimation, with the software program MARK (White and Burnham, 1999). To determine the best model that properly fit the data set, two tests were used to evaluate the models. A χ^2 test was used first to test the null hypothesis that each model fit the data. The χ^2 statistic was calculated by: $\sum_{i,j} \frac{(r_{ij} - E(r_{ij}))^2}{E(r_{ij})}$. The degrees of freedom (df) for each model type are: (1) $I(I+1)/2 + (J-I)I - (I+J-1)$ for model S_b, f_t ; (2) $I(I+1)/2 + (J-I)I - (J+1)$ for model S, f_t ; (3) $I(I+1)/2 + (J-I)I - J$ for model S_b, f ; and (4) $I(I+1)/2 + (J-I)I - 2$ for model S, f , where I is the number of years of tagging and J is the number of years of recovery (Brownie et al., 1985). A calculated χ^2 value (χ^2_{calc}) greater than the tabled value ($\chi^2_{df, 1-\alpha}$) indicates that the null hypothesis should be rejected.

Akaike Information Criterion (AIC) was also used to select the most parsimonious model, which is the model that best explains the variation in the data while using the fewest parameters (Akaike, 1973). AIC values were calculated for each model by: $-2\ln(L) + 2p$, where L is the maximized likelihood of the model and p is the number

of estimated parameters. Models were compared by calculating ΔAIC values by: $\Delta AIC = AIC_i - AIC_{min}$, where AIC_i is the AIC value for model i and AIC_{min} is the minimum AIC value over all models considered. Models that have small (< 2) ΔAIC values are well supported by the data (Williams et al., 2002). Among the models where ΔAIC was < 2 , the simpler, more restrictive model (the one that estimates the fewest number of parameters) was chosen for inference.

To check for overdispersion, the variance inflation factor, \hat{c} , was calculated in program MARK (White and Burnham, 1999) by the deviance divided by its degrees of freedom. The deviance of model j is defined as: $-2\ln(L_j) + 2\ln(L_{sat})$, where L_j is the maximum likelihood of model j and L_{sat} is the maximum likelihood of the saturated model (White and Burnham, 1999). The saturated model is the model where each tagged cohort has a different parameter value for each recapture cell. A value of \hat{c} is calculated for the most general model in a set of models under consideration, which in this study is Model S_b, f_i . Values of $\hat{c} > 1$ suggest overdispersion. Overdispersion is the existence of greater variation than theoretically predicted by the multinomial sampling model and can result from a lack of independence of recapture and survival events.

When overdispersion occurred (i.e., $\hat{c} > 1$), the quasi-likelihood AIC (QAIC) was

calculated by: $\frac{-2\ln(L)}{\hat{c}} + 2p$, and $\Delta QAIC$ values were calculated by: $QAIC_i - QAIC_{min}$,

where $QAIC_i$ is the QAIC value for model i and $QAIC_{min}$ is the minimum QAIC value over all models considered. The value of \hat{c} was also used to inflate the standard error of the parameter estimates in MARK (White and Burnham, 1999) by multiplying the standard error by the square root of \hat{c} (White et al., 2001).

Twice-a-year tagging models

Semi-annual estimates of survival were obtained by fitting a Brownie model analogous to model S_t, f_t in Table 1 to all the data. Tagging periods were specified as winter, 28 October to 13 March, and summer, 17 May to 28 August, while tag recovery periods were specified as winter, 28 October to 16 May, and summer, 17 May to 27 October. Thus there were seven tagging periods (4 winter and 3 summer) and seven recovery periods (4 winter and 3 summer) between October 2001 and May 2005. The four Brownie models fitted to the data were: (1) $S_{winter,t}, S_{summer,t}, f_{winter,t}, f_{summer,t}$, where survival and recovery rates in any period (winter or summer) vary over time, (2) $S_{winter}, S_{summer}, f_{winter}, f_{summer}$, where survival and recovery rates in any period (winter or summer) are constant over time, (3) $S_{winter,t} = S_{summer,t}, f_{winter,t}, f_{summer,t}$, where survival rates are constant over a year (i.e., that survival rates in winter and summer periods of a given year are the same), and recovery rates vary over time and (4) $S_{winter} = S_{summer}, f_{winter}, f_{summer}$, where survival rates are the same for all periods and recovery rates in any period (winter or summer) are constant over time. Models 3 and 4 tested the hypothesis that survival rates in winter and summer are equivalent. Since the amount of time encompassed in the winter and summer recapture periods differed, as winter rates were for 201 days (6.7 months) while summer rates were for 164 days (5.3 months), the time intervals in program MARK (White and Burnham, 1999) were set as 6.7 for the winter periods and 5.3 for the summer periods to obtain monthly estimates of survival. The estimates of tag recovery rate, f , obtained in program MARK (White and Burnham, 1999) refer to the period (i.e., they are not monthly rates). Model fit was assessed with the χ^2 goodness of fit test and models were compared using QAIC.

Tag-return assumptions

The assumptions of this study are: (1) the tagged crabs are representative of the target population, (2) tags are not shed, (3) survival rates are not affected by tagging, (4) the year of the recovery is reported correctly, (5) the fate of each tagged crab is independent, and (6) all tagged crabs within a cohort have the same annual survival and recovery rates (Brownie et al., 1985; Pine et al., 2003). The first assumption implies that newly tagged crabs should thoroughly mix with previously tagged crabs. Non-mixing among cohorts can result from a lack of dispersal immediately after tagging. In addition, tagged crabs should mix randomly with untagged crabs and have the same catchability. To avoid violating this assumption, tagging occurred over a wide area and in proportion to the catch rate (an indicator of abundance).

Fishing and natural mortality estimation

Estimates of fishing mortality (F) were obtained from Baranov's catch equation, $u = \left(\frac{F}{-\ln S} \right) \times (1 - S)$, by using female-specific estimates of u from the recent blue crab stock assessment (Miller et al.¹), S from our tagging study, and solving the equation for F . As described in the introduction, exploitation rates are based on comparing total catch during the year to estimates of abundance at the start of the year determined from the Bay-wide winter dredge survey (Sharov et al., 2003). The estimate of natural mortality (M) was obtained from the equation: $M = -\ln S - F$.

Tag reporting rate estimation

The tag recovery rate (f) can be modeled as $f = \phi \times \lambda \times u$, where ϕ is the probability a tagged animal does not shed the tag and does not die immediately after tagging, λ is the tag reporting rate or the probability that a fisher will report the capture of a tagged crab, and u is the exploitation rate or the proportion of the stock present at the start of the year that is caught during the year. As illustrated by McGarvey (2004), the tag reporting rate (λ) can be estimated when independent estimates of exploitation rate (u) are available. The tag reporting rate was estimated by using year specific values of f derived from fitting Brownie model S_b, f_i to the winter tagging data, by assuming that ϕ is equal to 1, and by using year and female specific exploitation rates obtained from the recent blue crab stock assessment (Miller et al.¹).

RESULTS

General recapture information

Totals of 219, 537, 985, and 647 crabs were tagged in the winters of 2001, 2002, 2003 and 2004, respectively (Table 2). During winter 2002, the majority of the tags used (520 of 537) were labeled with “Reward” rather than “\$20 Reward.” To determine if this had an effect on the tag recovery rates, Brownie model S_b, f_i was fitted to the data and the year-specific tag recovery rates were compared. The estimates of tag recovery rates for the first, second, third, and fourth years of the study were 27 %, 23 %, 25 % and 21 %, respectively. Since the recovery rates in all years were similar, we suspect that the labeling error did not greatly affect our estimates. Therefore, our analysis used all available tag data.

Of the 2388 crabs tagged during the winter periods, 598 were recaptured between 28 October 2001 and 27 October 2005 (Table 2). All but three of the recaptures were reported by commercial crabbers. Of the recaptures, 319 (53.3 %) were recaptured using crab pots and 262 (43.8 %) by crab dredge; the remainder was caught by assorted gear. Almost all recaptured crabs were caught inside of Chesapeake Bay (Figures 1, 2, 3, & 4). Recaptured crabs moved in all directions: towards the Bay mainstem, towards the edges of the mainstem, upriver, and downriver.

Of the 1320 crabs tagged during the summer periods, 239 were recaptured between 17 May 2002 and 16 May 2005 (Table 3). The majority of the recaptures, 228 (92 %), was reported by commercial crabbers, while the remainder was reported by recreational crabbers. Of the recaptures, 187 (78.2 %) were recaptured using crab pots, 27 (11.3 %) by crab dredge, and 20 (8.4 %) by trot line; the remainder was caught by assorted gear. Almost all recaptured crabs were caught inside of Chesapeake Bay (Figures 5, 6, & 7). Crabs released in the summer tended to be recaptured at locations downriver or down Bay from their release locations.

Annual survival

The goodness of fit test associated with all four Brownie models fitted to the winter tagging data suggested that the model fit was not adequate (Table 4). The poor fit was due to the recapture of one tagged animal in year 4 which was tagged in year 1 (cell r_{14} in the observed data matrix). If that one recapture is eliminated from the analysis (i.e., the r_{14} cell is changed from a 1 to a 0) all models would fit the data ($\chi^2_{calc} < \chi^2_{crit}$ for all models) and the calculated \hat{c} value would be < 1 . The model with the lowest AIC value

would be Model S, f . Although the probability of surviving the 3 years between year 1 and year 4 is very low, it is still possible, and therefore we decided to keep that recapture in the analysis. Due to the poor model fit, variance inflation factor was calculated by:

$$\hat{c} = \frac{-2\ln(L)_{S, f_i} + 2\ln(L)_{sat}}{df} = \frac{2918.76 - 2910.87}{3} = 2.63, \text{ and was used to calculate QAIC}$$

and ΔQAIC values and to adjust the standard errors associated with parameter estimates.

Model fit was adequate for all four Brownie models fitted to the summer tagging data (Table 4). The calculated \hat{c} value was < 1 ; therefore AIC and ΔAIC values were calculated.

For the winter tagging data, model (S, f) had the lowest ΔQAIC value (Table 4) and was thus selected for inference. For the summer tagging data, models (S, f) and (S, f_i) had ΔAIC values < 2.0 (Table 4). Therefore, model (S, f) was selected for inference because this model estimates the least number of parameters. Estimates of survival using model (S, f) derived from both the winter and summer tagging data were nearly identical (Winter data: $\hat{S} = 0.08 \pm 0.02$ SE, 95% CI: 0.04 – 0.13; Summer data: $\hat{S} = 0.08 \pm 0.02$ SE, 95% CI: 0.04 – 0.14). Tag recovery rate (\hat{f}) was estimated to be 0.24 ± 0.01 SE (95% CI: 0.21 – 0.27) and 0.17 ± 0.01 SE (95% CI: 0.15 – 0.19) based on the winter and summer tagging data, respectively.

Semi-annual survival

The goodness of fit test associated with the four Brownie models fitted to the twice-a-year tagging data (Table 5) suggested that the model fit was not adequate (Table 6). Similar to the once-a-year winter tagging data, the poor fit was due to the recapture of

one tagged animal in period 7 which was tagged in year 1 (cell r_{17} in the observed data matrix). If that one recapture is eliminated from the analysis (i.e., the r_{17} cell is changed from a 1 to a 0), then models 1 and 2 would fit the data (i.e., $\chi^2_{calc} < \chi^2_{crit}$) but models 3 and 4 would not. The calculated \hat{c} value would be 1.06 and the model with the lowest QAIC value would be Model ($S_{winter,t}, S_{summer,t}, f_{winter,t}, f_{summer,t}$). As before, we decided to keep that recapture in the analysis. Due to the poor model fit, variance inflation factor was calculated by:

$$\hat{c} = \frac{-2 \ln(L_{S_{winter,t}, S_{summer,t}, f_{winter,t}, f_{summer,t}}) + 2 \ln(L)_{sat}}{df} = \frac{4842.08 - 4824.71}{11} = 1.58, \text{ and was used}$$

to calculate QAIC and Δ QAIC values and to adjust the standard errors associated with parameter estimates.

Models ($S_{winter,t} = S_{summer,t}, f_{winter,t}, f_{summer,t}$) and ($S_{winter} = S_{summer}, f_{winter}, f_{summer}$) had high Δ QAIC values (9.26 and 15.36, respectively; Table 6) suggesting that survival rates in winter and summer were not equivalent. Model ($S_{winter}, S_{summer}, f_{winter}, f_{summer}$) had the lowest QAIC value and was thus chosen for inference. Estimated monthly rates of survival during the winter period (28 October to 16 May) were 0.87 ± 0.02 (95 % CI: 0.83 – 0.90), while monthly rates of survival during the summer period (17 May to 28 October) were estimated to be 0.74 ± 0.02 (95 % CI: 0.70 – 0.78). Given that the amount of time encompassed in the winter (6.7 mos) and summer (5.3 mos) periods differed, these monthly rates could be converted into period rates by: $\hat{S}_{winter}^{6.7}$ and $\hat{S}_{summer}^{5.3}$, respectively. The estimated rate of survival over the winter period was 0.39, while the estimated rate over the summer period was 0.20. In addition, an annual survival rate was estimated by the product of the two semi-annual rates, $\hat{S} = \hat{S}_{winter} \times \hat{S}_{summer} = 0.39 \times 0.20 =$

0.08. The estimated tag recovery rate for the winter period was 0.19 ± 0.01 (95 % CI: 0.17 – 0.21) while the estimated tag recovery rate for the summer period was 0.13 ± 0.01 (95 % CI: 0.11 – 0.16).

Estimates of fishing and natural mortality

Female-specific estimates of u for 2002 and 2003 were 0.64 and 0.55, respectively (Miller et al.¹). Estimates of S for 2002 and 2003 (0.07 and 0.09, respectively) were obtained from the winter tagging data fitted to Brownie model S_b, f_i . Fishing mortality rate (F) was estimated to be 1.83 and 1.46 in 2002 and 2003, respectively; natural mortality rate (M) was estimated at 0.83 and 0.95 in 2002 and 2003, respectively.

Tag reporting rate estimation

Estimates of λ were calculated by using the female-specific estimates of u for 2002 and 2003 (0.64 and 0.55, respectively (Miller et al.¹)), the estimates of f for 2002 and 2003 (0.27 and 0.23, respectively) obtained by fitting Brownie model S_b, f_i to the winter tagging data, and assuming ϕ is 1. Estimates of λ were the same for 2002 and 2003, 0.42, and relatively high considering that the blue crab fishery is mostly commercial.

Tag retention

To determine if tags remain intact when exposed to brackish water over the long term, 24 tags were attached to bricks and placed in the York River, Virginia, USA, in

March 2004 and were routinely checked. All tags were retained after 1.5 years of exposure to brackish water (salinity 20 - 22 ‰).

DISCUSSION

The two independent estimates of survival based on winter tagging (0.08 ± 0.02 SE) and summer tagging (0.08 ± 0.02 SE) were virtually identical and very low. These estimates were also similar to our estimates based on the product of two semi-annual estimates of survival. The question is whether such a low survival is credible and consistent with other data. Note first that we had excellent cooperation from the fishers, as evidenced by the high (24 % based on winter tagging and 17 % based on summer tagging) tag recovery rate during each of the years of the study. Previous studies obtained overall recovery rates of 6 to 12 % (Fiedler, 1930; McConaugha⁶; Turner et al., 2003; Aguilar et al., 2005) for similar tags used on blue crabs in Chesapeake Bay. Therefore, the low number of returns from cohort 1 in years 2, 3, and 4, from cohort 2 in years 3 and 4, and from cohort 3 in year 4 was not due to lack of cooperation in years 2, 3, and 4.

In addition, one might question whether a significant fraction of the tagged crabs might have emigrated outside Chesapeake Bay which, if progressive over time, would cause survival rate to be underestimated. However, a concurrent field investigation of crab abundance inside and outside Chesapeake Bay between January and March 2003 demonstrated that a very small proportion of the blue crab population resided outside of

⁶ McConaugha J. R. 1991. Tag-recapture study of the spawning stock of Chesapeake Bay blue crabs. 30 p. Technical report No. 91-1. Old Dominion University Research Foundation, Old Dominion University, Dept. of Oceanography, Norfolk, VA 23529.

the Bay proper (Lipcius et al.⁷). While tagging studies have documented a few cases where adult blue crabs have emigrated outside of Chesapeake Bay (Cronin, 1949; McConaughy⁶; Aguilar et al., 2005), it is generally considered that adult blue crabs limit their movements to within an estuary (Fischler and Walburg, 1962; Judy and Dudley, 1970). Thus, we believe that our estimates for survival rate were not biased significantly by statistical, biological, or environmental conditions. In addition, we believe our results were not biased by tag loss, as all tags that were attached to bricks remained intact after long term exposure (> 1.5 years) to brackish water.

The goodness of fit tests associated with all four Brownie models fitted to the winter tagging data (Table 4) and with the four models fitted to the twice-a-year tagging data (Table 6) suggest that the model fit was not adequate. The poor fit was due to the recapture of one tagged animal in year 4, which was tagged in year 1. This is common in tag return data as values in the rightmost cells in the matrix of expected values are often very small. Analysis was conducted despite the lack of model fit since the lack of fit was due to the recovery of a single crab. Although the probability of surviving the 3 years between year 1 and year 4 is very low, it is still possible. The variance inflation factor, \hat{c} , was used to adjust standard errors associated with parameter estimates to account for the lack of fit.

Ideally, all tag releases for a cohort would have occurred within a short time period. Since this was not logistically possible, the releases occurred over a longer time “window.” This introduces some bias since crabs that are released first will experience

⁷ Lipcius, R. N., J. M. Hoenig, and J. F. Walter. 2003. Spatial distribution of the blue crab in the Lower Chesapeake Bay-Continental Shelf System. Final Report to Army Corps of Engineers, Norfolk Branch. Virginia Institute of Marine Science, PO Box 1346, Gloucester Point, VA 23602.

more fishing and natural mortality than those released later. For example, the winter tagging occurred between late October and March. Crabs released towards the end of the winter would have less of a chance to be recaptured during the first year simply because they are at large for a shorter time period. If the probability of being recaptured in the first year of tag recovery is reduced as the time window of releases increases, the survival rates will be overestimated. The bias, however, may not be substantial since tagging in the winter occurred first in the mainstem of the Bay and then in the rivers (which are closed to fishing in the winter).

Our low estimates of survival are consistent with historical estimates of the percentage of 2+ females in the Bay-wide winter dredge survey and winter dredge fishery. Several studies have shown that in winter the percentage of adult females that have already spawned (and are therefore age 2+) is relatively low, suggesting that relatively few females survive through their second winter as adults (Hopkins, 1947; Williams and Porter, 1964; Haner et al.⁸; Newcombe⁹). The presence and condition of the nemertean, *Carcinonemertes carcinophila*, is a good indication of previous spawning (Hopkins, 1947). The nemertean lives on the gills of female crabs, but becomes sexually mature only on the egg mass on which it feeds (Humes, 1942). The sexually immature form of the nemertean is small and either white or pinkish, while the mature form is larger and bright red. A study that examined adult females captured in the Bay-wide

⁸ Haner J., R. N. Lipcius, and M. M. Montane (unpubl. data) Ovarian development, Nemertean infestation and spawning history of adult female blue crabs, *Callinectes sapidus*, in Chesapeake Bay. Virginia Institute of Marine Science, PO Box 1346, Gloucester Point, VA 23062.

⁹ Newcomb C. L. 1945. 1944-1945 Report of the Virginia Fisheries Laboratory. In Forty-sixth and forty-seventh annual reports of the Commission of Fisheries of Virginia, for the fiscal years ending June 30, 1944 and June 30, 1945. Division of purchase and printing, Richmond, VA. Virginia Institute of Marine Science, PO Box 1346, Gloucester Point, VA 23062.

winter dredge survey in the early 1990s found that very few females were infested with the adult form of the nemertean (Haner et al.⁸) suggesting that only a few had previously spawned. This further suggests that few females survived longer than 2+ years in the presence of the historical commercial fishery.

In samples of catches from crab dredge boats taken during the winters of the early 1940s, Newcombe⁹ indicated that only 6 % of adult females in the lower Bay had already spawned (and were therefore age 2+) as indicated by ovary condition. Williams and Porter (1964) examined 114 female crabs from the catch of a commercial crabber in Delaware Bay in September of 1954, of which only 6 % had spawned one or more times as indicated by ovary condition and presence of mature *C. carcinophila*. Hopkins (1947) examined ovaries of overwintering mature female crabs in Virginia waters in the mid 1940s and concluded that crabs that had not yet spawned were predominant. Only 8 of 107 crabs (7 %) examined had evidence of previous spawning as indicated by the appearance of egg remnants, exhausted ovaries, and condition of nemertean infestation (Hopkins, 1947). In contrast, Sette and Fiedler (1925) state that 33 % (47/144) of females examined in the winter had egg remnants attached to the swimmerets and therefore had previously spawned. However, the use of “egg remnants” as indicators of spawning history is questionable, as more recent analyses indicate that sediment particles can appear as “egg remnants” in crabs that bury in the sediment when overwintering (Lipcius¹⁰). The collective data indicate that previously spawned females (age 2+) comprise a relatively small portion of the female population which suggests relatively high annual mortality historically.

¹⁰ Lipcius, R. 2005. unpubl. data. Virginia Institute of Marine Science, PO Box 1346, Gloucester Point, VA 23602.

The maximum age of blue crabs, although not known precisely, is relatively short which further supports a low annual survival rate. Tag return data has provided evidence that blue crabs can live as long as 4 years in St. John's River, Florida (Tagatz, 1968), 5 years in North Carolina (Fishler, 1965), and 8 years in Chesapeake Bay (Rugolo et al., 1998). Various values for maximum age have been used in blue crab stock assessments, including 3 years for the Delaware Bay stock (Kahn and Helser, 2005), 3, 5 and 8 years for the North Carolina stock (Eggleston et al.¹¹), 3 and 6 years for stocks in Florida (Murphy et al.¹²), and 8 years for the Chesapeake Bay stock (Rugolo et al., 1998). In our tagging study, we recovered one tag (Tag A00145) in December of 2004, almost 3 years after it was released in January of 2002. Given that the crab was 1+ or 2+ years old at tagging, since the age of maturity is 1+ or 2+ years depending on whether the crab matures in the northern or southern portions of the Bay (Van Engel, 1958), this crab is estimated to have lived for at least 4 years, and possibly 5 years.

Our estimates of annual survival are much lower than what was once thought. Using an assumed natural mortality rate of 0.375 yr^{-1} and the female-specific exploitation rate estimates from 2002 and 2003 (0.64, 0.55, respectively; Miller et al.¹) to solve for F using methods described in Sharov et al. (2003), the estimates of survival ($S = e^{-(0.375+F)}$) for 2002 and 2003 are 0.18 and 0.25, respectively. There are several important issues to

¹¹ Eggleston, D. B., E. G. Johnson, and J. Hightower. 2004. Population dynamics and stock assessment of the blue crab in North Carolina. Final Report for contract 99-FEG-10 and 00-FEG-11 to the North Carolina Fishery Research Grant Program, North Carolina Sea Grant, and the North Carolina Department of Environmental Health and Natural Resources, Division of Marine Fisheries. North Carolina Sea Grant, NC State University, 100-B 1911 Building, Campus Box 8605, Raleigh, NC 27695.

¹² Murphy, M. D., C. A. Meyer, and A. L. McMillen-Jackson. 2001. A stock assessment for blue crab, *Callinectes sapidus*, in Florida waters, 56 p. FMRI (Florida Marine Research Institute) In house Report Series IHR 2001-008. Florida Fish and Wildlife Conservation Commission, FMRI, 100 Eighth Avenue SE, St. Petersburg, FL 33701.

consider when comparing these results of survival (18 % – 25 %) to the results from the present study (8 % survival). First, the results based on the exploitation rate method (“Sharov’s method”) do not account for recreational landings of crabs and thus u may be biased low, resulting in an underestimate of F and an overestimate of S ; the tagging results include all sources of mortality. Secondly, our estimates of survival are only for adult females, while the exploitation rate is based on the abundance of all female crabs that are legal size or are going to become legal size during the year. Thirdly, the estimates of u are for the years 2002 and 2003, while our estimates of survival are for the time period 10/28/01 to 10/27/02 and 10/28/02 to 10/27/03. While the timing relating to the two parameters is not the same, it is relatively close. Most importantly, Sharov et al. (2003) assumed a value of 0.375 yr^{-1} for M , whereas the tagging estimates of survival do not depend on knowledge of M . Results from the recent stock assessment suggest that a more likely value for natural mortality is 0.9 yr^{-1} (Miller et al.¹). Therefore, using an M of 0.9 yr^{-1} and using the same methods described above to estimate F from the exploitation rate, the estimates of survival ($S = e^{-(0.9+F)}$) for adult females for 2002 and 2003 are 0.06 and 0.10, respectively. Tagging-based estimates of survival are thus similar to estimates derived from the exploitation rate method when the assumed value of M is 0.9 yr^{-1} . Although tagging based estimates of S are not strictly comparable to those based on the exploitation rate method (Sharov et al, 2003), both indicate that survival was extremely low in recent years and much lower than that estimated by the last blue crab stock assessment (which estimated S based on a length-based method; \hat{S} ranged from 0.22 to 0.43 between 1956 and 1995; Rugolo et al., 1998). It would be ideal to compare estimates of exploitation rate to tag-based estimates of survival over several years to

determine if changes in one are tracked by changes in the other. If it were found that the estimates tracked each other, then this would serve as a form of validation of tag-based estimates of survival and dredge-survey derived estimates of exploitation.

Twice a year tagging allowed for estimation of semi-annual survival rates. Hearn et al. (1998) demonstrated the use of pre- and post-season tagging to estimate fishing and natural mortality for a species subject to a short pulse fishery. The blue crab fishery operates all year long and therefore models described by Hearn et al. (1998) would not be appropriate. This study provides possibly the only known use of a Brownie model to estimate semi-annual survival rates for an invertebrate species subject to a continuous fishery.

Survival during the winter months was much higher than it was during the summer months, which could reflect trends in exploitation or seasonal changes in natural mortality rate. Similarly, the annual tag recovery rate obtained from the once-a-year Brownie model fitted to the winter tagging data ($\hat{f} = 0.24$) was higher than the annual tag recovery rate from the once-a-year Brownie model fitted to the summer tagging data ($\hat{f} = 0.17$). The relatively low recovery rates obtained from summer data could reflect tag-induced mortality in the summer months. Crabs that are tagged in the summer are often exposed to extremely hot air temperatures (range: 27 °C – 38 °C) during tagging which could increase the probability of dying immediately after tagging. Provided that tagging induced mortality is consistent from summer to summer, this does not bias the estimates of survival.

The estimates of female-specific M , 0.83 yr⁻¹ and 0.95 yr⁻¹ in 2002 and 2003, respectively, are much higher than the currently assumed value of M of 0.375 yr⁻¹ in

Chesapeake Bay (Rugolo et al., 1998). These estimates were obtained by first deriving estimates of F from Baranov's Catch equation, $u = \frac{F}{-\ln S} \times (1 - S)$, by using female-specific estimates of u , and S from our tagging study. Then estimates of M were obtained by subtracting F from $-\ln S$. As previously discussed, it is important to note that the Bay-wide winter dredge survey estimates of exploitation are not directly comparable to our estimates of annual survival based on tagging. Although the types of data used to generate the estimates of u and S differ, this general approach was previously used by Kahn and Helser (2005) in an assessment of the blue crab stock in Delaware Bay.

While tag reporting rates (λ) can be theoretically estimated from Brownie models that are parameterized in terms of instantaneous rates of fishing and natural mortality, the estimates of λ are often unreliable (Hoenig et al., 1998) and therefore additional information is needed to obtain reliable estimates. Tag reporting rate can be estimated by: (1) using two types of tags, standard tags and high reward tags, and assuming a 100 % reporting rate for the high-reward tags (Pollock et al., 1991), and (2) secretly planting tagged animals into catches (Costello and Allen, 1968; Green et al., 1983; Hampton, 1997; Hearn et al., 2003). This study and McGarvey (2004) are the only known studies that have estimated tag reporting rate based on estimates of tag recapture rate, f , and external estimates of exploitation rate, u . We estimated the annual tag reporting rate to be 42 % for the time periods between 28 October 2001 to 27 October 2002 and 28 October 2002 to 27 October 2003. The consistent and relatively high tag reporting rate illustrates good cooperation from the fishers and indicates a reliable tag return program.

Tag-return methodology has proven to be an effective means of estimating the annual and semi-annual rates of survival for adult female blue crabs. This study provides

the only known experimentally derived estimate of survival for the blue crab. Other estimates of survival are based on length-based methods or on methods that are heavily dependent on an assumption that M is known. In addition, this study provides the only known use of a Brownie model to estimate semi-annual survival rates for an invertebrate species subject to a continuous fishery. Finally, the two independent estimates of annual survival based on winter and summer tagging were essentially the same and low. Consequently, low survival rates of mature female blue crabs in Chesapeake Bay during a period of low abundance may be preventing stock recovery.

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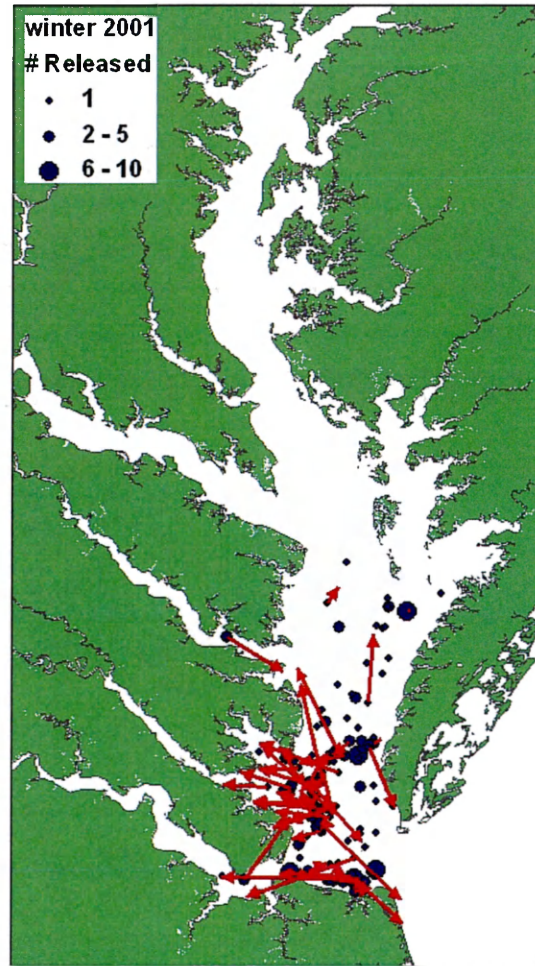
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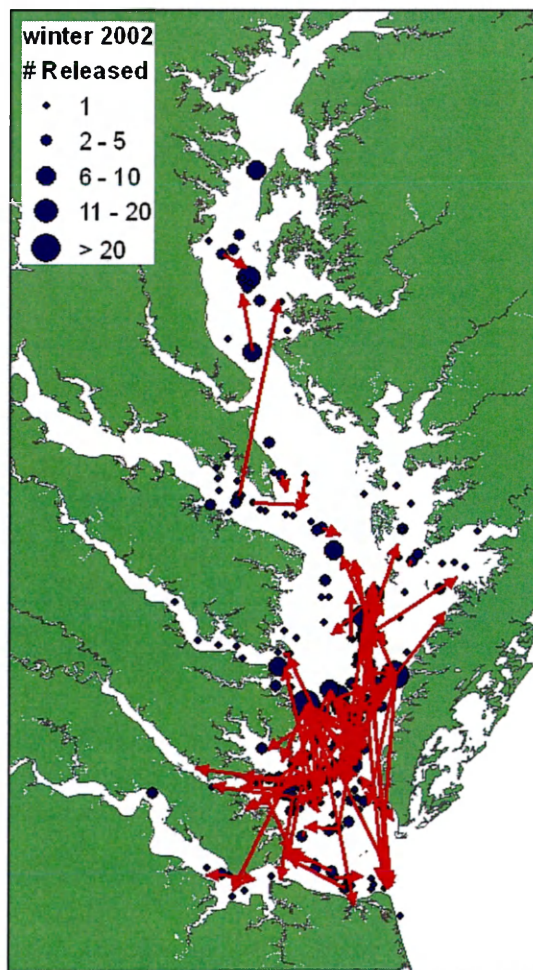
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Figure 1. Release and recapture locations for crabs tagged in winter 2001.



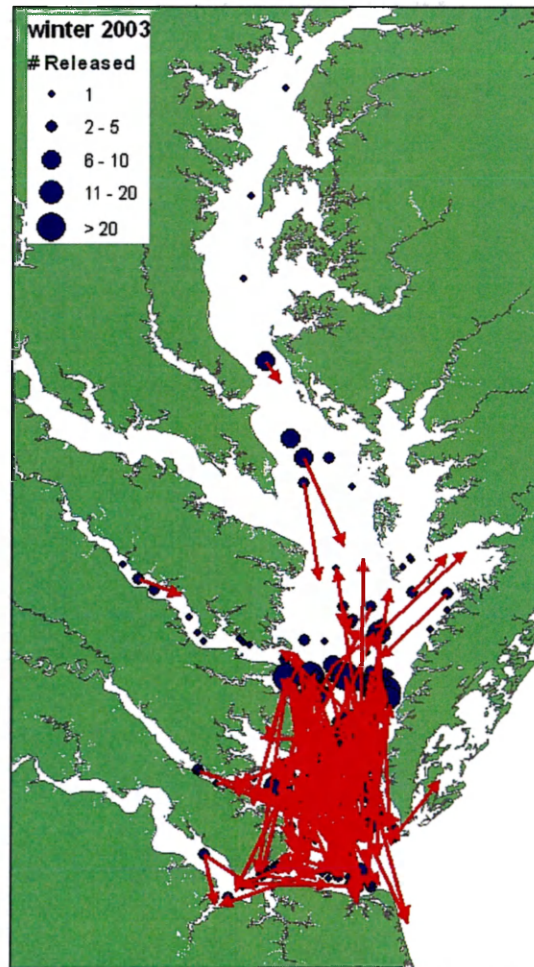
Blue circles indicate release location; the size of the circles refers to the number released at each location. The red arrows point to the recapture locations.

Figure 2. Release and recapture locations for crabs tagged in winter 2002.



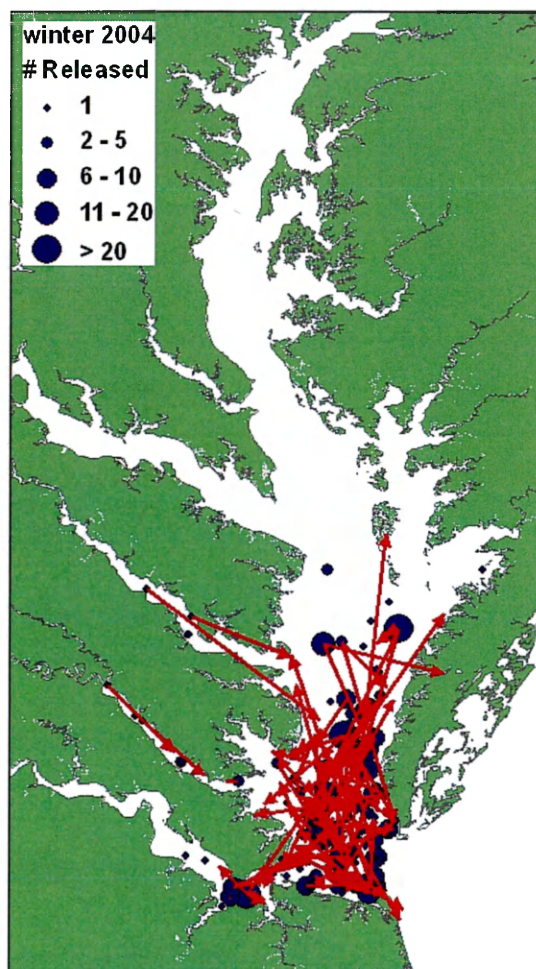
Blue circles indicate release location; the size of the circles refers to the number released at each location. The red arrows point to the recapture locations.

Figure 3. Release and recapture locations for crabs tagged in winter 2003.



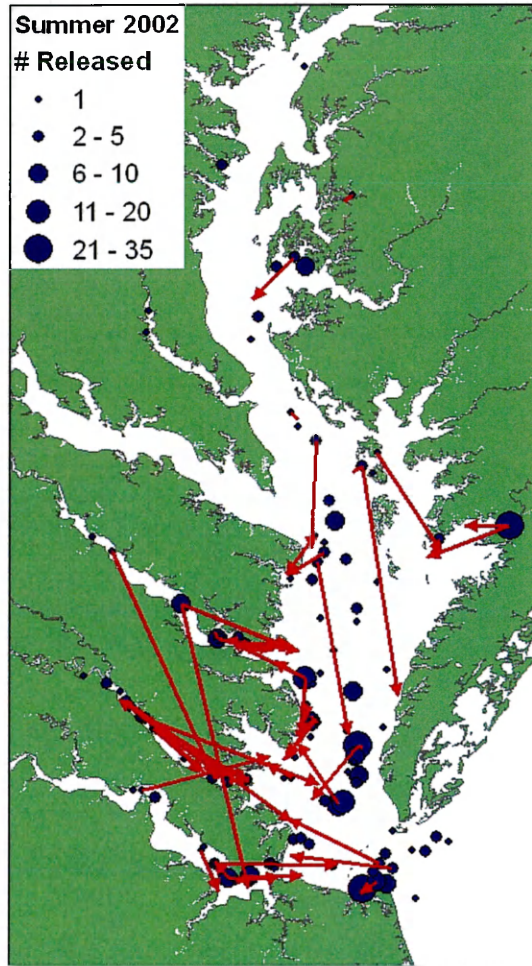
Blue circles indicate release location; the size of the circles refers to the number released at each location. The red arrows point to the recapture locations.

Figure 4. Release and recapture locations for crabs tagged in winter 2004.



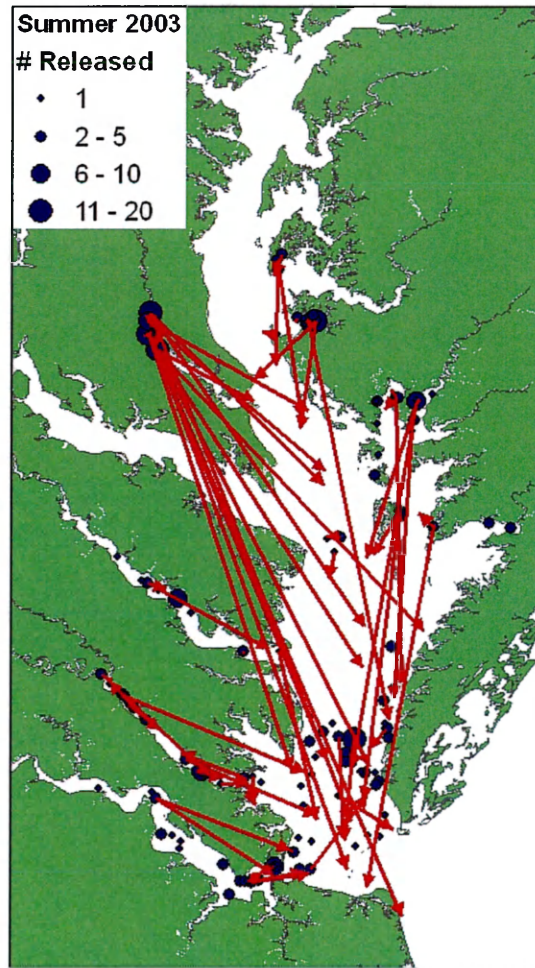
Blue circles indicate release location; the size of the circles refers to the number released at each location. The red arrows point to the recapture locations.

Figure 5. Release and recapture locations for crabs tagged in summer 2002.



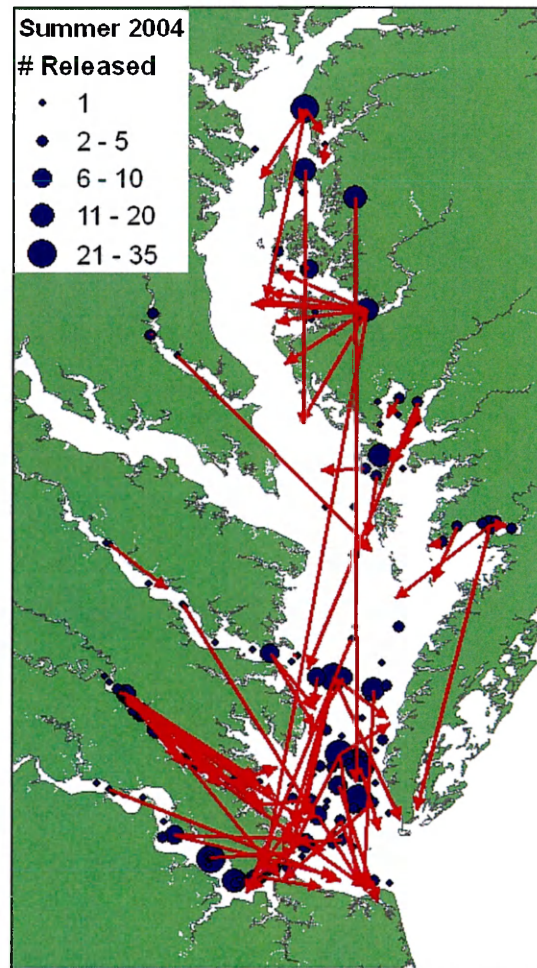
Blue circles indicate release location; the size of the circles refers to the number released at each location. The red arrows point to the recapture locations.

Figure 6. Release and recapture locations for crabs tagged in summer 2003.



Blue circles indicate release location; the size of the circles refers to the number released at each location. The red arrows point to the recapture locations.

Figure 7. Release and recapture locations for crabs tagged in summer 2004.



Blue circles indicate release location; the size of the circles refers to the number released at each location. The red arrows point to the recapture locations.

Table 1. Observed and expected number of tag recoveries from a Brownie model in which the parameters vary by year (Model $S_n f_n$); crabs were tagged in $I = 4$ years and recovered in $J = 4$ years.

year	# tagged	recoveries in year (j)			
		1	2	3	4
tagged (i)					
Observed recoveries, r_{ij}					
1	N_1	r_{11}	r_{12}	r_{13}	r_{14}
2	N_2	—	r_{22}	r_{23}	r_{24}
3	N_3	—	—	r_{33}	r_{34}
4	N_4	—	—	—	r_{44}
Expected number of recoveries, $E(r_{ij})$					
1	N_1	$N_1 f_1$	$N_1 S_1 f_2$	$N_1 S_1 S_2 f_3$	$N_1 S_1 S_2 S_3 f_4$
2	N_2	—	$N_2 f_2$	$N_2 S_2 f_3$	$N_2 S_2 S_3 f_4$
3	N_3	—	—	$N_3 f_3$	$N_3 S_3 f_4$
4	N_4	—	—	—	$N_4 f_4$

Table 2. Observed tag recoveries for adult female blue crabs that were tagged during the winter.

cohort	number tagged	Number recovered in year:			
		28 Oct 2001 - 27 Oct 2002	28 Oct 2002 - 27 Oct 2003	28 Oct 2003 - 27 Oct 2004	28 Oct 2004 - 27 Oct 2005
winter 2001	219	60	2	1	1
winter 2002	537	--	125	10	1
winter 2003	985	--	--	245	14
winter 2004	647	--	--	--	139

Data for cohorts winter 2001, winter 2002, winter 2003, and winter 2004 refer to crabs tagged between 28 October 2001 to 13 March 2002, 28 October 2002 to 13 March 2003, 28 October 2003 to 13 March 2004, and 28 October 2004 to 13 March 2005, respectively.

Table 3. Observed tag recoveries for adult female blue crabs that were tagged during the summer (between 17 May and 28 August of each year).

		Number recovered in year:		
cohort	number	17 May 2002 -	17 May 2003 -	17 May 2004 -
	tagged	16 May 2003	16 May 2004	16 May 2005
summer 2002	388	57	5	0
summer 2003	343	--	71	6
summer 2004	589	--	--	100

Table 4. Goodness of fit and Akaike Information Criterion (AIC) results.

Source	Model	Goodness of fit				# of parameters	-2ln(L)	QAIC	ΔQAIC	AIC	ΔAIC
		χ^2_{calc}	$\chi^2_{critical}$	df	p						
Winter	(S_b, f_i)	46.25	7.81	3	<0.0001	7	2918.76	1123.79	8.12		
	(S, f_i)	45.40	11.07	5	<0.0001	5	2919.10	1119.92	4.25		N/A
	(S_b, f)	47.66	12.59	6	<0.0001	4	2922.91	1119.37	3.70		
	(S, f)	50.01	15.51	8	<0.0001	2	2923.68	1115.67	0.00		
Summer	(S_b, f_i)	0.42	3.84	1	0.52	5	1320.55			1330.55	1.32
	(S, f_i)	1.16	5.99	2	0.56	4	1321.23		N/A	1329.23	0.00
	(S_b, f)	5.20	7.81	3	0.16	3	1325.34			1331.34	2.11
	(S, f)	5.62	9.49	4	0.23	2	1325.74			1329.74	0.51

The χ^2 calculated value (χ^2_{calc}), χ^2 critical value ($\chi^2_{df, 1-\alpha}$), degrees of freedom (df), p value, number of estimable parameters, and -2ln(L) are for four different Brownie models fitted to the winter and summer tagging data. For the winter tagging data, the calculated variance inflation factor ($\hat{c} = 2.63$) was > 1 indicating overdispersion, therefore QAIC and Δ QAIC were calculated to account for the lack of model fit. For the summer tagging data, AIC and Δ AIC were calculated since $\hat{c} < 1$.

Table 5. Tag recoveries for a twice-a-year tagging study where tagging was conducted in the winter and summer.

Cohort	# Tagged	Number recaptured in period:						
		Winter 28 Oct 2001 - 16 May 2002	Summer 17 May - 27 Oct 2002	Winter 28 Oct 2002 - 16 May 2003	Summer 17 May - 27 Oct 2003	Winter 28 Oct 2003 - 16 May 2004	Summer 17 May - 27 Oct 2004	Winter 28 Oct 2004 - 16 May 2005
winter 2001	219	54	6	2	0	1	0	1
summer 2002	388		50	7	2	3	0	0
winter 2002	537			88	37	7	3	1
summer 2003	343				51	20	4	2
winter 2003	985					199	46	14
summer 2004	589						79	21
winter 2004	647							108

Data for cohorts winter 2001, winter 2002, winter 2003, and winter 2004 refer to crabs tagged between 28 October 2001 to 13 March 2002, 28 October 2002 to 13 March 2003, 28 October 2003 to 13 March 2004, and 28 October 2004 to 13 March 2005, respectively. Summer tagging was conducted between 17 May and 28 August of each year.

Table 6. Goodness of fit and Akaike Information Criterion (AIC) results for the twice-a-year tagging data.

model	Goodness of fit				number of			ΔQAIC
	χ^2_{calc}	$\chi^2_{critical}$	df	p	parameters	$-2\ln(L)$	QAIC	
$S_{winter,b} S_{summer,b} f_{winter,b} f_{summer,t}$	82.46	25.00	15	<0.0001	13	4842.08	3090.61	3.69
$S_{winter} S_{summer} f_{winter} f_{summer}$	76.36	36.42	24	<0.0001	4	4864.70	3086.92	0.00
$S_{winter,t} = S_{summer,b} f_{winter,b} f_{summer,t}$	118.10	28.87	18	<0.0001	10	4860.37	3096.18	9.26
$S_{winter} = S_{summer} f_{winter} f_{summer}$	99.23	37.65	25	<0.0001	3	4892.13	3102.28	15.36

The calculated variance inflation factor ($\hat{c} = 1.58$) was > 1 , indicating overdispersion, therefore QAIC and ΔQAIC were calculated to account for the lack of model fit.

CHAPTER 3: ASSESSING EFFECTIVENESS OF THE BLUE CRAB SPAWNING
STOCK SANCTUARY IN CHESAPEAKE BAY USING TAG-RETURN
METHODOLOGY

CHAPTER 3: ASSESSING EFFECTIVENESS OF THE BLUE CRAB SPAWNING STOCK SANCTUARY IN CHESAPEAKE BAY USING TAG-RETURN METHODOLOGY

ABSTRACT

The blue crab spawning stock in Chesapeake Bay sustained a severe and persistent decline beginning in 1992. As part of the effort to enhance the spawning stock, the spawning sanctuary in lower Chesapeake Bay was enlarged to over 240,000 ha. This marine reserve and corridor prohibits exploitation of mature females en route to or in the spawning grounds during the summer spawning season (1 June-15 September). To assess the effectiveness of the sanctuary, we tagged terminally molted, mature females inside and outside the sanctuary during three sanctuary seasons (2002-2004). Crabs were captured throughout the Bay and its tributaries, measured, tagged, and released on site. Recaptures of tagged crabs were reported by commercial and recreational fishers. Probability of recapture for crabs released outside of the sanctuary was 6.3, 5.2, and 2.8 times the probability of recapture for crabs tagged inside the sanctuary for 2002, 2003 and 2004, respectively. Consequently, a significant proportion of adult female blue crabs remains in the sanctuary to spawn and is not captured by the fishery. Hence, the marine reserve and corridor for the blue crab spawning stock in Chesapeake Bay is an effective means of protecting females migrating to or residing in the spawning grounds. This investigation serves as one of the few empirical tests to date of the effectiveness of a

marine reserve designed to protect spawning stock.

INTRODUCTION

Marine Protected Areas and Terminology

The term “marine protected area” (MPA) is a broad term that refers to a marine area that has been reserved by law to protect part or all of the resources within its boundaries (www.mpa.gov). The goals of a MPA may range from the protection of cultural or historical heritage, the conservation of biodiversity, and the promotion of sustainable fisheries. In addition, the level of protection within MPAs may vary from restricting human access, restricting impact, to prohibiting extraction. MPAs that prohibit the extraction of biological resources are referred to as marine reserves or no-take zones (NRC 2001). Spawning stock reserves (also referred to as spawning sanctuaries or sanctuaries) are a type of marine reserve that is designed to specifically protect the spawning stock of a species. Corridors refer to a linear landscape that allows movement between habitat patches (Rosenberg et al. 1997).

Spawning stock reserves

One of the main objectives of marine reserves is the protection of spawning-stock biomass to provide a source of recruitment to fisheries outside the reserve via larval dispersal (Roberts & Polunin 1991, Dungan & Davis 1993, Rowley 1994). Marine reserves will enhance or maintain recruitment in unprotected areas only when stock sizes in those areas are very low while the stock size in the protected area remains high (Roberts & Polunin 1991). Assessment of the effectiveness of marine reserves is important to improve the design, use and management of reserve systems. Assessment

typically involves definition of the goals and objectives of the reserve, collection of data on various measurable indicators of success, and evaluation to determine whether the reserve is meeting the intended goals and objectives.

Empirical evidence for the efficacy of reserves that specifically target the spawning stock (i.e., spawning stock reserves) is extremely limited. The presumption that spawning stock reserves will increase recruitment in nearby areas is often not valid (Kassner & Malouf 1982, Helsinga 1984, McCay 1988), probably due to various biotic and physical processes critical to enhancing recruitment at the metapopulation level (Lipcius et al. 2005). Examples of effective marine reserves do exist however. Spawning stock abundance and potential egg production were higher in reserves than outside reserves for the spiny lobster, *Panulirus argus*, (Bertelsen & Cox 2001, Lipcius et al. 2001a), the American lobster, *Homarus americanus*, (Rowe 2002), and the Nassau grouper, *Epinephelus striatus*, (reviewed in Chiappone & Sealey 2000), which were most likely linked to the higher abundance and larger sizes of animals in reserves. Although it is uncertain whether an increase in egg production or spawning stock abundance will lead to an increase in recruitment, these studies suggest the feasibility of protecting a portion of the spawning stock in reserves to enhance egg production of marine metapopulations.

The transplanting of adult animals into desired areas with the goal of increasing recruitment has been conducted with several invertebrates, including the hard clam, *Mercenaria mercenaria*, (Kassner & Malouf 1982, McCay 1988), wild-caught (Southworth & Mann 1998) and hatchery produced (Brumbaugh et al. 2000) oysters, *Crassostrea virginica*, green abalone, *Haliotis fulgens*, (Tegner 1992), and queen conch, *Strombus gigas* (Delgado et al. 2004). Indicators of success in these studies included

various measures such as survival rates of transplants, breeding and spawning potential within the reserves, reproductive behavior, egg production, gonadal condition, larval abundance, and subsequent abundance of recruits and juveniles. The transplanting of clams was deemed ineffective when clam abundance, survival, and gamete production of the transplanted clams were low (McCay 1988) or when contribution to larval production and recruitment was low (Kassner & Malouf 1982). The transplanting of oysters onto no-take oyster reefs has seen occasional success throughout Chesapeake Bay, as spat settlement has increased on some stocked reefs and nearby oyster grounds following stocking efforts (Southworth & Mann 1998, Brumbaugh et al. 2000). Low mortality and evidence of reproduction, based on a visual index of gonadal bulk, of transplants and large numbers of apparent recruits suggest that the transplanting of green abalone can be effective in enhancing populations (Tegner 1992). The translocation of non-spawning adult conch to offshore sites, where spawning occurs, has been shown to be a potential means of augmenting the spawning stock (Delgado et al. 2004).

The protection of spawning aggregations is another means of using marine reserves to protect spawning stock. Since spawning aggregations are often predictable and targeted by fishers, they are susceptible to overexploitation. In some cases protection of spawning aggregations has increased density, biomass and individual size of various grouper species (Beets & Friedlander 1992, 1998, Chiappone et al. 2000). Protection of spawning aggregations has also resulted in a more favorable sex ratio in the red hind, *Epinephelus guttatus*, (Beets & Friedlander 1992, 1998), gag, *Mycteroperca microlepis*, and scamp, *M. phenax* (Coleman et al. 2004).

Tag-return studies, where animals are captured, tagged and released with the hope that they are recaptured and reported at some future date by the commercial or recreational fishery, have been used to assess the movement of animals in relation to marine reserves. Tag-return data can be used to estimate emigration rates of animals from reserves (Attwood & Bennett 1994, McGarvey 2004), to demonstrate the movement of juveniles away from protected nursery habitats into areas open to exploitation (Davis & Dodrill 1980, 1989, Gitschlag 1986), and to compare recapture rates between animals tagged inside and outside of reserves (Rowe 2001, Medici 2004). When tag-return studies are conducted concurrently in areas open to fishing and in marine reserves, patch-specific mortality rates can be estimated (Joe 2001).

Blue crab, *Callinectes sapidus*

Mature female blue crabs are ideal for tag-return studies because they do not molt (Churchill 1919, Van Engel 1958) so tag loss is likely to be minimal. The shape of the carapace is such that a light-weight and non-invasive tag can easily be attached around the lateral spines on the dorsal surface. Tag-return studies on the blue crab have been used to examine migration in coastal Texas (Benefield & Linton 1990), Florida (Tagatz 1968, Osterling 1976), South Carolina (Fischler & Walburg 1962), North Carolina (Fischler 1965, Judy & Dudley 1970, Medici 2004), Chesapeake Bay (Fiedler 1930, Truitt 1936, 1939, Cronin 1949, McConaughy 1991, 1993, Turner et al. 2003, Aguilar et al. 2005), and Delaware Bay (Cronin 1954). In addition, tag-return studies on blue crabs have provided estimates of population size (Fischler 1965) and an assessment of the effectiveness of protected areas in North Carolina (Medici 2004). It was the objective of

this study to use tag-return methodology with adult female blue crabs in Chesapeake Bay to assess the effectiveness of the Virginia blue crab spawning sanctuary.

The blue crab fishery is the most important commercial fishery in Chesapeake Bay (Rugolo et al. 1998; Anon. 2003), yet spawning stock biomass has declined by 84 % relative to levels in the late 1980s (Lipcius & Stockhausen 2002). The life cycle of the blue crab in Chesapeake Bay involves a terminal molt of the females and subsequent mating between early May and October with peaks in May and late August or early September (Van Engel 1958, Millikin & Williams 1984). After maturing and mating, female crabs migrate to the southern portion of Chesapeake Bay either to spawn or to overwinter and spawn the following year (Churchill 1919, Van Engel 1958). Spawning occurs between May and early September (Van Engel 1958, Jones et al. 1990, Prager 1996).

History of the blue crab sanctuary

One approach to managing the blue crab stock in Chesapeake Bay involves a marine reserve. A spawning sanctuary established in the southern portion of the Bay in 1941 was originally 37,814 ha (Figure 1; Rob O'Reilly, Virginia Marine Resources Commission (VMRC), personal communication) and closed to the crab fishery during July and August (Sandoz 1943). The sanctuary was originally implemented in response to a significant decline in blue crab harvest throughout the Chesapeake Bay in 1940 and 1941 and was established to protect adult female blue crabs during the spawning period (Sandoz 1943). The sanctuary season was extended to include April, May, and June in 1943 (Sandoz 1943). Initial investigations deemed the historical sanctuary effective due

to high densities of blue crab zoeae (Sandoz 1943, Newcombe 1943), migration of egg-bearing female crabs (Sandoz 1943, Newcombe 1943), and optimal environmental conditions for embryonic and larval development (Sandoz & Rogers 1944) in the sanctuary area. In addition, our evaluation of data from a previous tag-return study (McConaugha 1993) indicated that adult female crabs tagged within the historical sanctuary were not captured by the fishery.

It is not known when the sanctuary season switched to the present day period of 1 June to 15 September. Commercial crab harvesting is prohibited in the sanctuary area between 1 June and 15 September; recreational crabbing is lawful only in the lower Bay area of the sanctuary (Section 28.2-709 of the Code of Virginia). The size of the sanctuary has increased considerably over the last 12 years. In 1994, the Bayside Eastern Shore Sanctuary (BESS) was established to include an additional 19,400 ha of protected waters in the Bay along the eastern shore of the lower Bay, which was later reduced to 16,000 ha in 1998 when the upper portion was removed and opened to fishing (Figure 1; Seitz et al. 2001). Approximately 16 % of the potential spawning stock was protected by the historical sanctuary and BESS (Seitz et al. 2001), however this was not a sufficiently large enough fraction of the spawning stock to avert an 84 % decrease in spawning stock biomass (Lipcius & Stockhausen 2002) relative to levels before 1992.

Lipcius et al. (2001b) studied the potential for an expanded sanctuary which incorporated a deepwater dispersal corridor in protecting adult female crabs. The term corridor is used in wildlife ecology studies to refer to a linear landscape that allows movement between habitat patches (Rosenberg et al. 1997). For the blue crab, the deepwater corridor in the mainstem of the Bay would function to protect females from

harvest as they migrate to the spawning grounds in the lower Bay. Lipcius et al. (2001b) found catch per unit effort (CPUE) of adult females in a fishery independent trawl survey was significantly higher in the proposed deepwater marine reserve and corridor (> 13 m depths) than in adjacent shallow water, suggesting that expansion of the existing sanctuary into deeper waters would further protect the spawning stock.

In June of 2000, the sanctuary was expanded from the mouth of the Bay to the Virginia/Maryland border, roughly following the 10.7 m depth contour in the mainstem of the Bay, to a size of 172,235 ha (Figure 2; Lipcius et al. 2003). The purpose of the expansion was not only to protect those female crabs in the spawning grounds but also to protect adult females en route to the spawning grounds during the reproductive period. Approximately 50 % of the adult females sampled by Lipcius et al. (2003) occurred in waters deeper than 10 m and were therefore protected by the spawning sanctuary. The Virginia blue crab sanctuary was enlarged again in 2002, roughly following the 9.1 m depth contour, to its current size of 240,092 ha (Figure 2; VMRC Regulation # 4 VAC 20-752-10 ET SEQ). The enlarged sanctuary is estimated to protect 70% of the adult females (i.e. spawning stock) in lower Chesapeake Bay during the spawning season (Lipcius et al. 2003). The effectiveness of the current sanctuary, however, had not been addressed, and it provided an opportunity to assess the efficacy of a marine reserve in protecting the spawning stock of a heavily exploited marine species.

The objective of the blue crab spawning sanctuary is to protect females in and en route to the spawning grounds in the reproductive period with the overall goal of increasing spawning potential. The effectiveness of the sanctuary in protecting the blue crab is in part determined by the degree and nature of crabs' mobility relative to the size

and shape of the sanctuary. The effectiveness of the sanctuary is dependent on female crabs remaining in the sanctuary for spawning, and would be reduced if females were to move outside of the sanctuary prior to spawning and become captured by the fishery. To assess the effectiveness of the spawning sanctuary, mature females were tagged and released inside and outside of the sanctuary in the summers of 2002, 2003, and 2004. A comparison of the probability of recapture for crabs tagged outside the sanctuary to crabs tagged inside the sanctuary using relative risk provided a means of assessing sanctuary effectiveness quantitatively.

METHODS

Tagging and tag return

Mature female crabs were obtained from the Virginia Institute of Marine Science (VIMS) Trawl Survey, Maryland Department of Natural Resources (MDNR) Trawl Survey, and VIMS Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAAP) between 1 June and 15 July of 2002, 2003, and 2004. The Chesapeake Biological Laboratory (CBL) Chesapeake Bay Fishery Independent Multispecies Fisheries Survey (CHESFIMS) also obtained crabs in 2004. Crabs were measured (carapace width, spine tip to spine tip) with vernier calipers and tagged by tying a strap tag across the back and around the lateral spines (Figure 3); the ends were crimped together with a 0.635 cm, zinc-plated-copper, oval sleeve (mean weight of tag and crimp = 1.27 ± 0.06 SD g). Crabs were then released as close as possible to the capture location (Figures 4 & 5). The number of tagged crabs released at each site was proportional to the

number caught at the site, which helped ensure that the distribution of tagged crabs was representative of the distribution of mature females. Each tag had an individual identification number, a toll-free phone number, the words "\$20 REWARD" and instructions to record the location and date of capture. An informational flyer was sent in February 2004 to all licensed crab fishers in Virginia to inform them of the tagging program. Newspaper articles in the Waterman's Gazette (published by the Maryland Watermen's Association) also publicized the program regularly since July 2004.

Captures of tagged crabs were reported by commercial and recreational fishers, who either left a message on the tag reporting phone line or spoke directly with staff at VIMS. We obtained as much of the following information over the phone as possible: location of capture, date of capture, water depth, method of capture, presence or absence of an egg mass, and whether the fisher was commercial or recreational. A letter describing the program with the corresponding crab release information, a data sheet, a map of the Chesapeake Bay, and a self-addressed stamped envelope were mailed to the fisher with instructions to make any additional comments, to mark the location of the capture, and to return the data forms and tag back to VIMS. Once the tag was received, payment was mailed to the fisher.

Survey Design

The VIMS Trawl Survey operates in the Virginia portion of the Bay and in the James, York, and Rappahannock Rivers. The survey deploys a 9.14 m semi-balloon otter trawl and tows for 5 min at approximately 100 sites monthly according to a combined fixed and stratified random sampling design (Montane et al. 2004). The MDNR Trawl

Survey samples 37 fixed sites in six river systems (Chester River, Eastern Bay, Choptank River, Patuxent River, Tangier Sound, and Pocomoke Sound) and 12 trial sites in three river systems (Fishing Bay, Little Choptank, and Nanticoke) monthly from May through October using a 4.9 m semi-balloon otter trawl (L. Fegley, Maryland Department of Natural Resources, personal communication).

The VIMS ChesMMAAP survey samples the entire mainstem of the Chesapeake Bay, stratifying the bay into five regions with three depth strata per region. The survey deploys a 13.7 m otter trawl and tows at approximately 3.5 knots for 20 min per site. Five cruises are conducted each year (March, May, July, September, and November) and approximately 80-90 sites are sampled per cruise (Latour et al. 2003, Bonzek et al. 2004).

The CHESFIMS survey, conducted by University of Maryland, Chesapeake Biological Laboratory, conducts three cruises a year (spring, summer, and fall) and samples approximately 50 sites per cruise throughout the mainstem of the Bay according to a combined fixed and stratified random sampling design. The survey uses a single, oblique stepped midwater trawl (18 m²) (Miller et al. 2004).

Recapture probability

The effectiveness of the sanctuary was characterized by comparing the probability of recapture for crabs tagged outside the sanctuary to the probability of recapture for crabs tagged inside the sanctuary using relative risk (Daniel 1999). Only crabs tagged between 1 June and 15 July and then subsequently recaptured from 1 June to 15 September (the time period that the sanctuary is in effect) were considered for this analysis.

Relative risk (RR) is a ratio of two probabilities and is calculated by p_1/p_2 , where p_i is the proportion of the animals in group i that is recaptured and i takes on the values “tagged inside” and “tagged outside” the sanctuary. The 95 % confidence interval for the relative risk is calculated by:

$$RR^{1 \pm \left(z_{\alpha} / \sqrt{\chi^2} \right)},$$

where z_{α} is the two-sided z value corresponding to the chosen confidence interval ($z = 1.96$) and χ^2 is the Chi Squared test statistic (Daniel 1999). The χ^2 value derived from a 2 x 2 contingency table (comparing frequency of tagged crabs that are recaptured and not recaptured within the sanctuary and outside of the sanctuary) can be calculated by the shortcut formula:

$$\frac{n(ad - bc)^2}{(a + c)(b + d)(a + b)(c + d)},$$

where n is the total number of crabs tagged, and a, b, c, d are the number of crabs tagged outside and recaptured, number of crabs tagged outside and not recaptured, number of crabs tagged inside and recaptured, and number of crabs tagged inside and not recaptured, respectively (Daniel 1999). The null hypothesis is that tag recapture and location of release (inside vs. outside of the sanctuary) are independent. A relative risk of one indicates that the probability of recapture is the same for both groups of crabs, whereas a relative risk greater than one implies that the probability of recapture for crabs tagged outside is greater than that of crabs tagged inside.

The shortest in-water distance between release location and the sanctuary border was estimated using Arcview GIS software for each crab tagged and recaptured. Data were pooled across all years and probability of recapture was plotted against distance to

sanctuary border at release for both crabs tagged inside and outside of the sanctuary. This was conducted to determine if all crabs within an area, either inside or outside of the sanctuary, are equally likely to be recaptured regardless of the distance to the sanctuary border. The analysis for crabs released inside the sanctuary tests the biological hypothesis that crabs that are released close to the sanctuary border are more likely than those tagged deep within the sanctuary to be recaptured either by illegal fishing in the sanctuary or by moving outside the sanctuary and being recaptured legally. The analysis for crabs released outside of the sanctuary tests the biological hypothesis that crabs released closer to the sanctuary are more likely to move inside the sanctuary and are therefore less likely to be recaptured than those tagged far from the sanctuary.

Movement, distance traveled, and days at large

The recapture locations of tagged crabs were plotted using Arcview GIS software based on the location description provided by the fisher. Recapture locations are approximations as specific coordinates were rarely provided. Migration of crabs was assessed qualitatively by plotting straight lines between release and recapture locations. The shortest possible in-water distance between release location and recapture location was estimated using Arcview GIS software. These distances were likely underestimates of the actual distances traveled. The number of days at large (the number of days between release and subsequent recapture) was calculated for all recaptured crabs. Data were pooled from the three years; mean distance traveled and mean number of days at large were calculated for crabs released inside and outside the sanctuary. Unpaired t-tests

were conducted to determine if mean distance traveled and mean days at large varied with release location (inside vs. outside the sanctuary).

Size

The mean size (mm carapace width) of crabs tagged inside and outside of the spawning sanctuary during each year were compared using unpaired t-tests. To test at a nominal $\alpha = 0.05$, the individual tests were conducted at a Bonferroni-corrected $\alpha = 0.05/3 = 0.017$. In addition, size data over all years and both tagging locations were pooled, due to low sample size, and then the mean size of crabs that were and were not recaptured were compared with an unpaired t-test.

RESULTS

Recapture probability

A total of 843 crabs was released between 1 June and 15 July of 2002, 2003 and 2004, of which 104 crabs were recaptured during the time period of the sanctuary (1 June – 15 September). The majority of recaptures (92 %) was reported by commercial fishers, of which 94 % was recaptured in crab pots, 5 % by trot line, and 1 % within pound nets. The remaining 8 % of recaptures was reported by recreational fishers. Two of the commercial recaptures were reported by seafood picking houses rather than by individual fishers.

Crabs tagged outside of the sanctuary had significantly higher probabilities of recapture than those tagged inside the sanctuary in 2002 (RR = 6.3, 95 % CI 2.4 – 16.3)

and 2004 (RR = 2.8, 95 % CI 1.6 – 5.0) (Table 1). An increased risk of recapture was also detected in 2003 (RR = 5.2, 95 % CI 0.9 – 29.0), although this result was marginally significant (Table 1). For all three years, the percentage recaptured was much higher for crabs released outside of the sanctuary relative to crabs released inside the sanctuary, ranging from 12 – 21 % outside the sanctuary and 2 – 6 % inside the sanctuary (Table 1). There was no apparent relationship between distance to the sanctuary border and the probability of recapture for both crabs released inside or outside of the sanctuary (Figure 6).

Ideally, all tag releases would have occurred on the first day that the sanctuary was imposed (1 June) in each year. Since this was not logistically possible, the releases occurred over a longer time “window.” This introduces some bias since crabs that are released first will experience higher fishing mortality than those released later. Crabs released towards the end of the sanctuary season (i.e., in late August and September) would have less of a chance to be recaptured during the time period of the sanctuary, regardless of release location, simply because they are at large for a shorter time period. An analysis of the relative risk of recapture using different periods of release window length (as additional crabs were tagged after July 15 for another study) showed that the relative risk did not change substantially. We chose crabs tagged between 1 June and 15 July in our analysis because this time window for crab releases was short enough to reduce the potential for bias but it also provided an adequate sample size for analysis.

Movement, distance traveled, and days at large

Almost all recaptured crabs were caught at locations down river or down Bay from their release locations. Crabs that were tagged outside of the sanctuary moved towards the Bay mainstem and the lower Bay spawning grounds (Figure 4). Crabs released inside the sanctuary tended to be recaptured in the lower Bay spawning grounds and in shallow feeding areas (Figure 5).

The distance traveled by crabs varied from < 1 km to 135 km (mean = 26 ± 3 SE km, $n = 102$). No significant difference in distance traveled was detected between crabs released inside (mean = 23 ± 4 SE km, $n = 16$) and outside (mean = 27 ± 3 SE km, $n = 86$) the sanctuary (t-test: $df = 100$; $p = 0.596$).

The overall time at large for crabs recaptured during the sanctuary season varied from 1 to 48 d (mean = 15.04 ± 1.27 SE d, $n = 99$). The mean time at large was significantly longer for crabs released inside the sanctuary (23.18 ± 3.44 SE d, $n = 17$) than for crabs released outside the sanctuary (13.35 ± 1.28 SE d, $n = 82$) (t-test: $df = 97$; $p = 0.003$).

Size

The mean size (mm carapace width) of females released between 1 June and 15 July outside and inside of the spawning sanctuary differed by less than 3 mm and was not significantly different in 2002 (Table 2, t-test: $df = 193$; $p = 0.719$) and 2003 (Table 2, t-test: $df = 165$; $p = 0.225$). The mean size of crabs was significantly larger outside (148.4 ± 1.4 SE mm, $n = 209$) than inside (138.8 ± 1.1 SE mm, $n = 207$) the sanctuary in 2004 (Table 2, t-test: $df = 386$; $p < 0.0005$). Over all years and both tagging locations, the

mean size of crabs that were recaptured (144.7 ± 1.5 SE mm, $n = 101$) was significantly larger than the mean size of crabs that were not recaptured (140.8 ± 0.7 SE mm, $n = 677$) (t-test: $df = 776$; $p = 0.035$).

DISCUSSION

The effectiveness of marine reserves in protecting mobile species is determined by the degree and nature of their mobility and the size and shape of the reserve. Highly migratory species are more likely to move outside of protected areas and become susceptible to exploitation, such that large reserves are needed (Polacheck 1990, Rowley 1994, Gu  nette et al. 2000). Female blue crabs in Chesapeake Bay migrate up to 200 km (Fiedler 1930, Hines et al. 1995, Turner et al. 2003, Aguilar et al. 2005, this study) to reach the spawning grounds in the lower portion of the Bay. The blue crab spawning sanctuary encompasses 240,092 ha in the mainstem of lower Chesapeake Bay from 1 June to 15 September. The effectiveness of the sanctuary is dependent on female crabs remaining in the sanctuary for spawning, and would be reduced if females were to move outside the sanctuary and be exploited prior to spawning. The probability of recapture was substantially and significantly higher for crabs tagged outside the sanctuary relative to crabs tagged inside the sanctuary during the three years of this study, such that females outside the sanctuary were approximately 3-6 times more likely to be caught by fishers than females inside the sanctuary. These findings indicate that the sanctuary is of a sufficient size that most females in the sanctuary do not move out of the spawning sanctuary prior to spawning.

In addition, these results suggest that illegal fishing inside the sanctuary is low. Illegal recapture of a tagged crab should not deter the reporting of a crab because the illegitimacy of the recapture would be unknown and the \$20 reward offers considerable incentive for reporting. Moreover, we flew over the sanctuary at two different times during the summer of 2002, and observed very few crab pots within the sanctuary boundaries. Hence, the collective evidence indicates that the spawning sanctuary is effective in allowing a considerable fraction (approximately 70%, Lipcius et al. 2003) of the blue crab spawning stock that enters the sanctuary to spawn during the reproductive period in Chesapeake Bay. Furthermore, our estimate of the effectiveness of the sanctuary is likely an underestimate because females tagged outside the sanctuary could move inside the sanctuary during migration to the spawning grounds and therefore would not be susceptible to the fishery. This would reduce the probability of recapture for crabs tagged outside the sanctuary and would lower the relative risk of recapture, therefore underestimating the effectiveness of the sanctuary.

There was no apparent relationship between the distance to the sanctuary border and the probability of recapture for crabs released inside (or outside) of the sanctuary, suggesting that degree of protection does not depend critically on location within the sanctuary. This further supports the idea that the sanctuary is of a proper design and large enough, relative to the movements of females, to protect the females within its borders.

This is the only known study that has demonstrated the use of relative risk as a tool to assess the effectiveness of a marine reserve. Tag-return data have, however, been used to compare percent recapture between animals tagged inside and outside of reserves

(Rowe 2001, Medici 2004). Rowe (2001) tagged American lobster, *Homarus americanus*, inside and outside of two small reserves in Newfoundland, Canada. Only 0 - 19 % of lobsters tagged inside the reserve were recaptured by the fishery, as opposed to a 12 - 72 % recapture rate of lobsters tagged in areas open to the fishery (Rowe 2001). Medici (2004) compared the percentage recaptured of blue crabs tagged inside and outside two small spawning sanctuaries located at inlets along the Outer Banks of North Carolina along the Western Atlantic Ocean. The proportions recaptured from the different locations were approximately equal, indicating that the relatively small spawning sanctuaries offered little protection to the blue crab spawning stock in that system. The ineffectiveness of these sanctuaries was likely due to their small size (1,798 ha and 3,539 ha) relative to the movement patterns of adult females (Anonymous 2004, Medici 2004).

Our findings provided further evidence for the migration of adult female blue crabs down the tributaries and mainstem of the Bay towards the spawning grounds during late spring and summer. Although the mean distance traveled did not vary between crabs tagged inside and outside the sanctuary, crabs tagged inside the sanctuary were at large for a significantly longer time than crabs tagged outside the sanctuary. This suggests that even though crabs in the sanctuary may be captured by the fishery, they remain in the system for a longer period of time and therefore are more likely to spawn than crabs outside the sanctuary.

The mean size of the crabs that were recaptured was significantly larger than the mean size of the crabs that were not recaptured. This could be related to the size-selective exploitation due to the use of cull rings in the commercial fishery (Lipcius &

Stockhausen 2002). Cull rings are used in crab pots throughout the tributaries and mainstem of the lower portion of Chesapeake Bay and in the mainstem of the upper portion of the Bay, which allows smaller adult females (i.e. < 140 mm carapace width) to escape pots, while larger females are captured in the crab pots (Guillory & Hein 1998).

The sizes of crabs tagged inside and outside of the sanctuary did not differ significantly in 2002 and 2003, but in 2004 females tagged inside the sanctuary were significantly smaller than those tagged outside (Table 2). If smaller females had a lower probability of recapture by the fishery (Guillory & Hein 1998, Lipcius & Stockhausen 2002), then the relative risk estimates would have been biased high in favor of the sanctuary in 2004.

Although the blue crab sanctuary is effective in protecting the females that have entered its borders, the sanctuary and various exploitation controls have not protected a sufficiently large fraction of the population (Seitz et al. 2001) to avert the 84 % decline in spawning stock biomass (Lipcius & Stockhausen 2002), sustained low abundances (Chesapeake Bay Stock Assessment Committee 2005), and low annual survival rates (see Chapter 2). There is thus an urgent need to restore the spawning stock for long-term, sustainable exploitation and population persistence of the blue crab in Chesapeake Bay. High fishing mortality of blue crab females outside of the sanctuary likely precludes sufficient numbers of mature females from successfully migrating to the spawning sanctuary, therefore limiting the benefits of the seasonal closure. The current management regime must be altered to increase the numbers of mature females entering the spawning sanctuary, through a combination of extended spatial management zones encompassing migration corridors and nursery grounds, as well as effort reductions in

fished areas. In addition, the expansion of the sanctuary through November and into the upper Bay would protect those females migrating from the upper portions of the Bay (Turner et al. 2003, Aguilar et al. 2005), while expanding it into April and into the upper Bay would protect females that have overwintered either in deep-water migration corridors or in the spawning grounds and will produce their first egg mass in the spring (Van Engel 1958, Millikin & Williams 1984).

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Table 1. Number of adult female blue crabs tagged and recaptured, percent recaptured, relative risk (95% Confidence Interval), Chi-Square test statistic (χ^2) ($\chi^2_{1,0.95} = 3.84$) and corresponding significance levels (p) for crabs tagged and released outside and inside of the spawning sanctuary between 1 June and 15 July and recaptured during the time that the sanctuary is in effect, for 2002, 2003, and 2004.

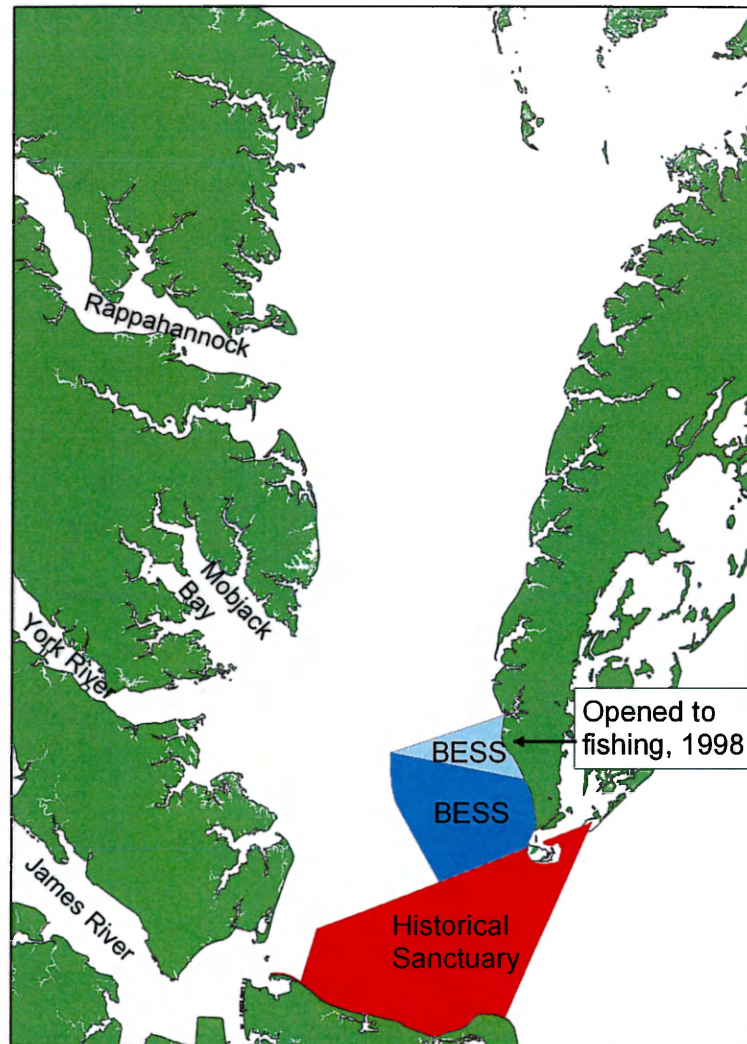
	tagging	number	number	%	relative		
year	location	tagged	recaptured	recaptured	risk	χ^2	p
2002	outside	168	35	21	6.3 (2.4, 16.3)	14.5	<0.0005
	inside	91	3	3			
	total	259	38	15			
2003	outside	125	15	12	5.2 (0.9, 29.0)	3.5	0.06
	inside	43	1	2			
	total	168	16	10			
2004	outside	209	37	18	2.8 (1.6, 5.0)	12.8	0.0003
	inside	207	13	6			
	total	416	50	12			

Table 2. Mean size (carapace width) and standard error (SE) of adult female blue crabs tagged and released outside and inside of the spawning sanctuary between 1 June and 15 July.

Year	Location	N	Mean size (mm)	SE	<i>p</i>
2002	outside	162	137.1	1.2	0.719
	inside	33	136.0	3.0	
2003	outside	124	141.4	1.3	0.225
	inside	43	138.5	1.9	
2004	outside	209	148.4	1.4	<0.0005
	inside	207	138.8	1.1	

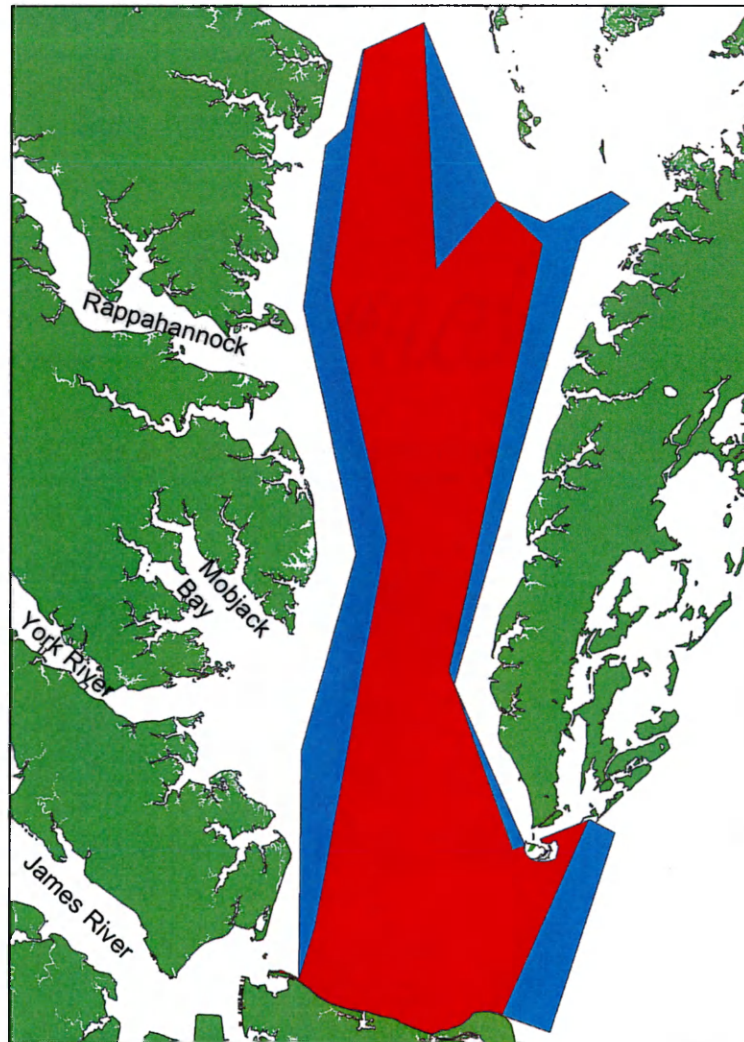
The sample sizes (N) may vary somewhat from those listed in Table 1 because some crabs were not measured.

Figure 1. Map of the historical spawning sanctuary (in red; created in 1941).



The sanctuary was expanded in 1994 to include the Bayside Eastern Shore Sanctuary (BESS). A portion of the BESS was opened to fishing in 1998.

Figure 2. Map of current spawning sanctuary.

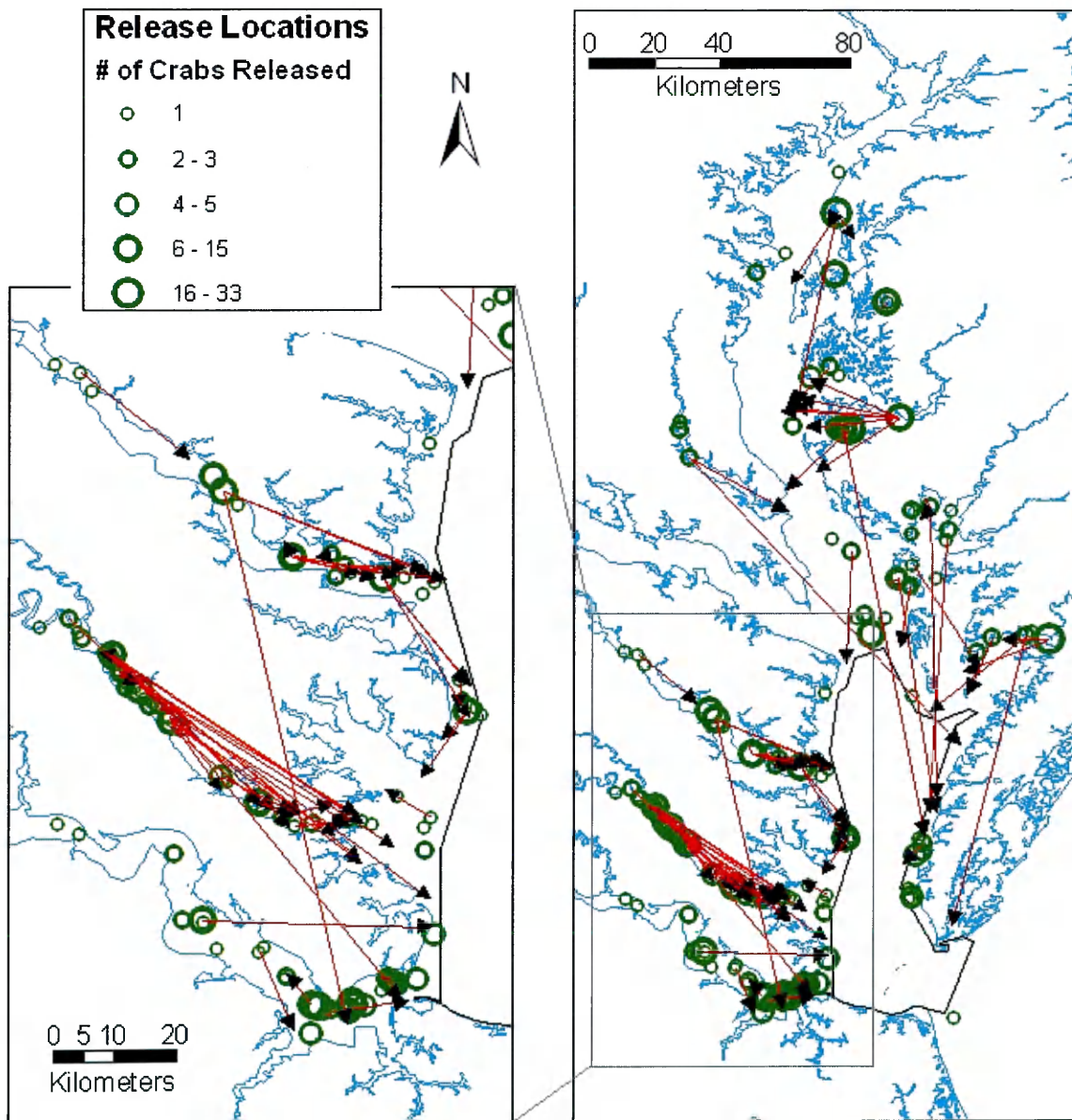


The area in red depicts the size of the sanctuary in 2000. In 2002, the sanctuary was enlarged to include the area in blue.

Figure 3. Mature blue crab female with tag attached.

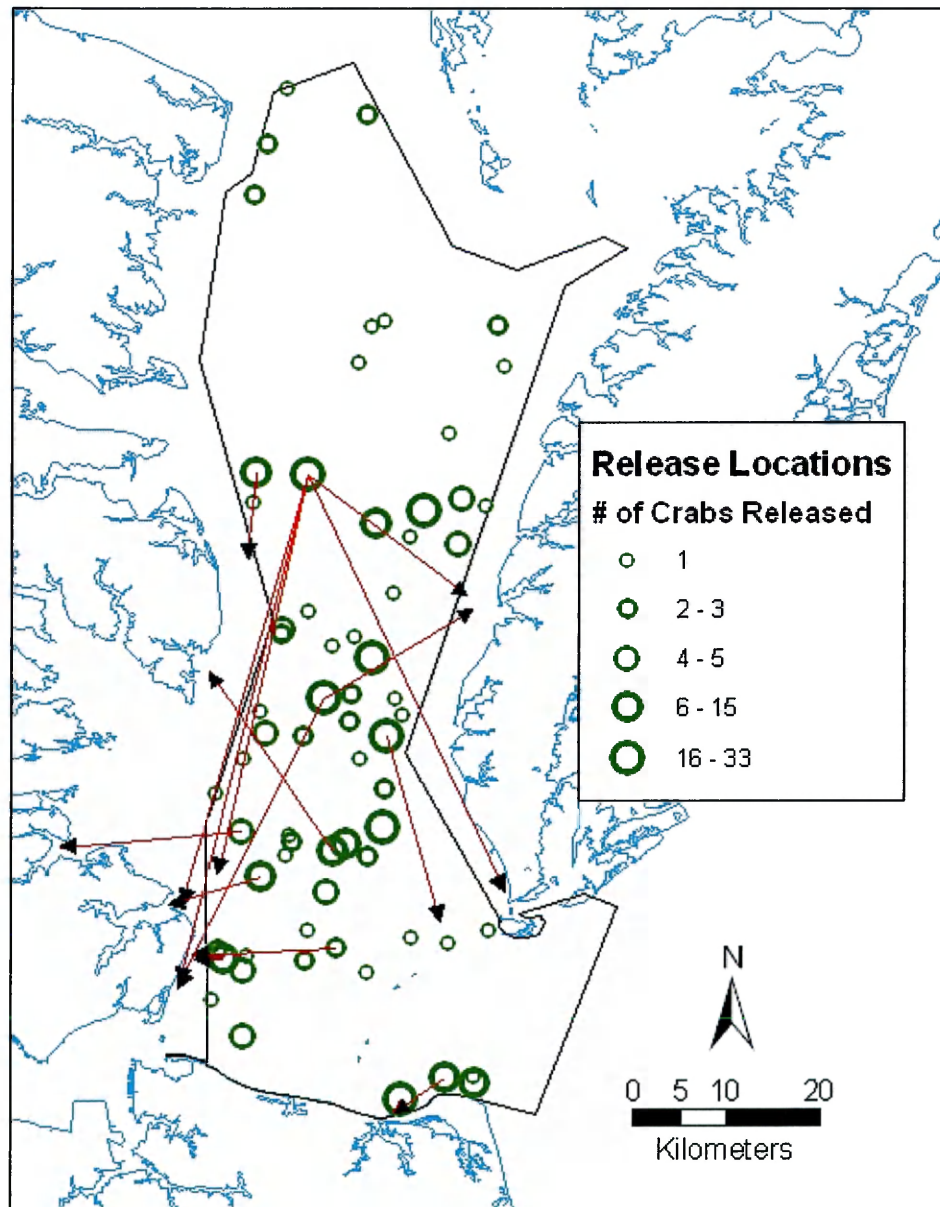


Figure 4. Map of release locations of mature female crabs tagged outside of the spawning sanctuary between 1 June – 15 July of 2002, 2003, and 2004.



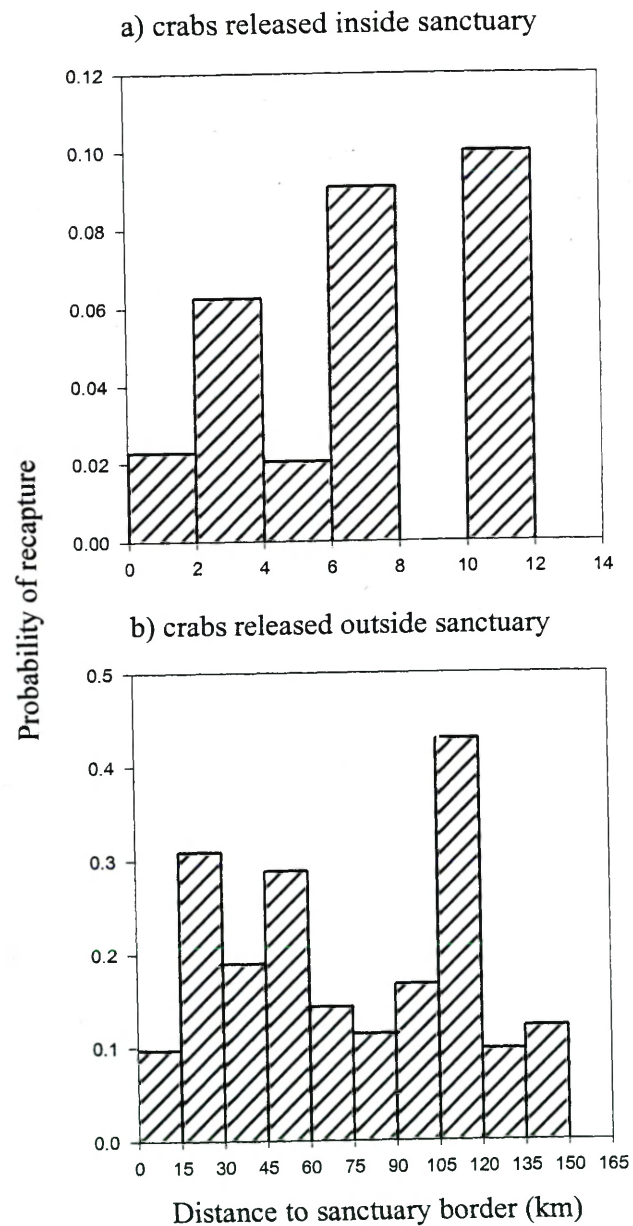
The size of the circles refers to the number of crabs released at each location. Lines with arrows indicate the recapture locations of individual crabs. The black outlined area represents the blue crab spawning sanctuary.

Figure 5. Map of release locations of mature female crabs tagged inside of the spawning sanctuary between 1 June – 15 July of 2002, 2003, and 2004.



The size of the circles refers to the number of crabs released at each location. Lines with arrows indicate the recapture locations of individual crabs. The black outlined area represents the blue crab spawning sanctuary.

Figure 6. Recapture probability of tagged crabs in relation to the distance to sanctuary border at release for (a) crabs released inside of the spawning sanctuary and (b) crabs released outside of the spawning sanctuary.



CHAPTER 4: CONCLUSIONS AND IMPLICATIONS

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Given the current focus on blue crab conservation in Chesapeake Bay and the emphasis of the blue crab stock assessment, there has been a need to obtain reliable field estimates of survival to compare to biological reference points. Tag-return methodology has proven to be an effective means of estimating annual and semi-annual rates of survival for adult female blue crabs. In this study, the two independent estimates of annual survival based on winter tagging ($\hat{S} = 0.08$) and summer tagging ($\hat{S} = 0.08$) were surprisingly similar and low. The low estimates of survival are consistent with historical estimates of the percentage of 2+ females in the Bay-wide winter dredge survey and winter dredge fishery. Several studies have shown that previously spawned females (age 2+) comprise a relatively small portion of the female population in the winter, suggesting relatively few females survive through their second winter as adults. The maximum age of blue crabs, although not known precisely, is relatively short which further supports a low annual survival rate.

This study provides the only known experimentally derived estimate of survival for the blue crab. Other estimates of survival have been based on length-based methods or on methods that are heavily dependent on an assumption that M is known. In addition, this study's estimates of annual survival were much lower than was once perceived. Using the previously assumed natural mortality rate of 0.375 yr^{-1} (Rugolo et al. 1998) and the female-specific exploitation rate estimates from 2002 and 2003 (0.64, 0.55,

respectively; Miller et al. 2005) to solve for F using methods described in Sharov et al. (2003), the estimates of survival ($S = e^{-(0.375+F)}$) for 2002 and 2003 are 0.18 and 0.25, respectively. Recent evidence suggests that a more likely value for natural mortality is 0.9 yr^{-1} (Helser and Kahn 1999, Miller et al. 2005, this study). Therefore, using an M of 0.9 yr^{-1} and using the same methods described above to estimate F from the exploitation rate, the estimates of survival ($S = e^{-(0.9+F)}$) for 2002 and 2003 are 0.06 and 0.10, respectively. Tagging-based estimates of survival are thus similar to estimates derived from the exploitation rate method when the assumed value of M is 0.9 yr^{-1} . It would be ideal to compare estimates of exploitation rate to tag-based estimates of survival over several years to determine if changes in one are tracked by changes in the other. If it were found that the estimates tracked each other, then this would serve as a form of validation of tag-based estimates of survival and dredge-survey derived estimates of exploitation.

This study also provides the only known semi-annual rates of survival for the blue crab. Survival during the winter months (monthly $\hat{S} = 0.87 \pm 0.02 \text{ SE}$) was higher than it was during the summer months (monthly $\hat{S} = 0.74 \pm 0.02 \text{ SE}$) which could reflect trends in exploitation or seasonal changes in natural mortality. In addition, the annual tag recovery rate obtained from the once-a-year Brownie model fitted to the winter tagging data ($\hat{f} = 0.24$) was higher than the annual tag recovery rate from the once-a-year Brownie model fitted to the summer tagging data ($\hat{f} = 0.17$). The relatively low recovery rate obtained from summer data could reflect tag-induced mortality in the summer months. This does not bias the estimates of survival rate, provided that tag-induced mortality is constant across years.

The estimates of female-specific natural mortality rate (M), 0.83 yr^{-1} in 2002 and 0.95 yr^{-1} in 2003, are much higher than the past assumed value of M of 0.375 yr^{-1} (Rugolo et al. 1998) in Chesapeake Bay. The biological reference points, which are critical to assessing the status of the blue crab stock, described by BBCAC (2001) were based on an assumed M of 0.375 yr^{-1} . The more recent blue crab stock assessment used 0.9 yr^{-1} for the likely value of M (Miller et al. 2005). Since exploitation rate differs between male and female crabs in the Bay, sex-specific estimates of F could be considered in the future (Miller et al. 2005). Tagging based estimates of F for the female portion of the stock could then be compared to target and threshold levels of F for females. Tag-return studies therefore have direct benefits to stock assessment in helping determine if management goals are being met and if overfishing is occurring.

Given that annual survival of adult female crabs has been low during a time of low spawning stock abundance, it is important that management measures implemented to protect the spawning stock be at least kept in place or possibly strengthened. The Virginia blue crab sanctuary was designed to protect female crabs during the spawning period. The effectiveness of the sanctuary is dependent on female crabs remaining in the sanctuary for spawning, and would be reduced if females were to move outside the sanctuary and be exploited prior to spawning. The probability of recapture was substantially and significantly higher for crabs tagged outside the sanctuary relative to crabs tagged inside the sanctuary during the three years of this study, such that females outside the sanctuary were approximately 3-6 times more likely to be caught by fishers than females inside the sanctuary. There was no relationship discernible between the distance to the sanctuary border and the probability of recapture for crabs released inside

(or outside) of the sanctuary, suggesting that the degree of protection does not depend critically on location within the sanctuary. Crabs tagged inside the sanctuary were at large for a significantly longer time than crabs tagged outside the sanctuary, which suggests that even though crabs in the sanctuary may be captured by the fishery, they remain in the system for a longer time and therefore are more likely to spawn than crabs outside the sanctuary.

These findings indicate that survival rates of mature female blue crabs in Chesapeake Bay have remained extremely low during a period of low abundance which may be preventing stock recovery. Although the blue crab sanctuary is effective in protecting the females that have entered its borders, it only offers protection for 3.5 months of the year and for a specific life-history stage—mature females. In addition, a low annual survival rate suggests that very few adult females live long enough to spawn in more than one year. The sanctuary and various exploitation controls have not protected a sufficiently large fraction of the population (Seitz et al. 2001) to avert the 84 % decline in spawning stock biomass relative to levels in the late 1980s (Lipcius & Stockhausen 2002), sustained low abundances (Chesapeake Bay Stock Assessment Committee 2005, Miller et al. 2005), and low annual survival rates (this study). There is thus an urgent need to restore the spawning stock for long-term, sustainable exploitation of the blue crab in Chesapeake Bay. High fishing mortality of blue crab females outside of the sanctuary likely precludes sufficient numbers of mature females from successfully migrating to the spawning sanctuary, therefore limiting the benefits of the seasonal closure. The current management regime could be altered to increase the numbers of mature females entering the spawning sanctuary, through a combination of extended

spatial management zones encompassing migration corridors and nursery grounds, as well as effort reductions in fished areas. In addition, the expansion of the sanctuary through November and into the upper Bay would protect those females migrating from the upper portions of the Bay (Turner et al. 2003, Aguilar et al. 2005), while expanding it into April and into the upper Bay would protect females that have overwintered either in deep-water migration corridors or in the spawning grounds and will produce their first egg mass in the spring (Van Engel 1958, Millikin & Williams 1984).

Tag-return methodology is a fruitful means of estimating survival and semi-annual survival in the blue crab. This study represents one of the few to derive field estimates of semi-annual survival of an invertebrate species subject to a continuous fishery using Brownie Models. This investigation also serves as one of the few empirical tests to date of the effectiveness of a marine reserve designed to protect the spawning stock. In addition, this is the only known study that has assessed the effectiveness of a management tool for the blue crab in Chesapeake Bay.

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